



RESEARCH ARTICLE

Inter-group relationships influence territorial defence in mountain gorillas

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Funding information

Dian Fossey Gorilla Fund

Handling Editor: Damien Farine

Abstract

1. Many species show territoriality, in which territory owners have exclusive or priority use of a region. In humans, tolerance of others within our space also depends greatly on our social relationships with them. This has been hypothesized as one potential driver of the evolution of long-term, inter-group relationships, through enabling shared access of resources and easing disputes over space.
2. However, extremely little is known about the importance of social relationships between neighbouring groups in non-humans for how space is used and shared.
3. Using 16 years of data on the simultaneous movement and interaction patterns of 17 mountain gorilla groups, we investigated how the occurrence of aggressive and affiliative behaviour during inter-group encounters was influenced by both their social and spatial context.
4. We found evidence of territorial defence, with rates of aggression increasing towards the centre of home ranges. Groups which had previously split from each other showed higher levels of affiliation during encounters with each other and experienced lower levels of aggression when within the other's peripheral home range. However, encounters within core areas of the home range consistently elicited higher aggression, regardless of the groups' history. Our findings indicate that not only are the social relationships between groups retained after they split from one another but also that these relationships enable groups to access certain areas with a reduced risk of aggression.
5. This suggests that reduced aggression when accessing areas within neighbours' home ranges may be an advantage for the maintenance of inter-group relationships and a potential driver in the evolution of long-term, post-dispersal relationships and complex multi-level societies.

KEYWORDS

aggression, inter-group dynamics, multi-level societies, neighbour, social evolution, space use, territoriality, tolerance

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1 | INTRODUCTION

Although definitions of territoriality have varied greatly, a territory is commonly defined as the area in which a territory owner has exclusive or priority access to resources (Hinsch & Komdeur, 2017; Maher & Lott, 1995). In some species, territories are held by individuals, while in many group-living species, communal territories are held by multiple individuals (Christensen & Radford, 2018). Territorial behaviours, such as scent marking, vocal advertisement, boundary patrols and aggression, are used to establish and maintain these territories (Boitani & Fuller, 2000). Demonstrating space-associated intolerance is therefore often used to confirm the presence of territorial defence (Eibl-Eibesfeldt, 1975; Vine, 1973), for example, through increased rates of aggression when encountering intruders in the more central regions of a home range (Bolyard & Rowland, 2000; Christensen & Radford, 2018; Crofoot et al., 2008; Furrer et al., 2011). Although in some species, where range overlap is minimal, aggressive territorial disputes are most common in more peripheral areas near territory boundaries, where the majority of inter-group encounters occur (Gittins, 1980; Sillero-Zubiri & Macdonald, 1998; Watts & Mitani, 2001). Territorial defence may also be further influenced by the resources present in the area, with greater defence of, and competition over, areas of high-resource quality (Johnsson et al., 2000; Pröhl & Berke, 2001).

In addition to location-specific factors, the decision to defend space can also vary depending on factors relating to the intruder, for example, the competitive ability of an opposing group in a potential dispute or the likelihood of interacting with them again (Hinsch & Komdeur, 2017; Maynard Smith & Price, 1973; Switzer et al., 2001). In certain species, rival males but not potential breeding partners are excluded from the territory (Boesch et al., 2008; Boitani & Fuller, 2000). Some species defend territories more strongly against neighbours (those with adjacent territories) compared to non-neighbours—known as the 'nasty neighbour' effect (Müller & Manser, 2007; Newey et al., 2010). In other species, the opposite has been found, with stronger defensive responses to non-neighbours—the 'dear enemy' effect (Christensen & Radford, 2018; Rosell & Bjørkøyli, 2002; Temeles, 1994). In species where neighbouring groups show varying degrees of home range overlap, this division between neighbour and stranger may be less clear cut, with both familiarity and the potential for competition declining with the degree of home range overlap or distance between home ranges.

In humans, territorial defence can vary considerably due to social relationships (Cashdan, 1983; Pisor & Surbeck, 2019; Vine, 1973). These take neighbour versus stranger responses a step further, not only discriminating between familiar and unfamiliar conspecifics but also showing clear preferences between familiar conspecifics. For example, in most modern human societies, an individual's reaction to unexpectedly finding a close friend in their home may differ drastically to their reaction to unexpectedly finding an acquaintance in their home. Similar patterns have been observed in many hunter-gatherer societies such as Aboriginal Australian groups (Peterson, 1975) and the San of the Kalahari (Cashdan, 1983) where

access to neighbouring groups' territories is primarily restricted to kin and those with close relationships. This has been proposed as a form of reciprocal altruism whereby preferred neighbouring groups can benefit from reciprocal access to resources within each other's ranges (Cashdan, 1983). Human social relationships can even influence access to geographical regions at far larger spatial scales, for example, in the ease with which certain nationalities can gain a visa to access a foreign country while others cannot. In humans, both the social and spatial context have considerable impact on the defence of space. Human territoriality is therefore suggested to be flexible to the social context and less strict than territoriality in many other species (Cashdan, 1983; Vine, 1973).

These inter-group relationships have been proposed to be beneficial for easing disputes over space and enabling improved resource access, with the potential to drive the evolution of long-term friendships (Brent et al., 2014) and complex social structure (Chapais, 2013; Pisor & Surbeck, 2019). However, extremely little is known about the importance of such social relationships for patterns of space use in any other species. This social element of territoriality has even been proposed as a unique product of human culture (Cashdan, 1983). Although an alternative explanation is that we have lacked the fine-scale data on inter-group encounters to detect these potentially quite subtle effects in any species but our own.

Humans have a multi-level social structure made up of hierarchically nested social units (Grueter et al., 2012), but the same underlying social structure has been reported in numerous large-brained social mammals. These include whales (Baird, 2000; Whitehead et al., 2012), elephants (Wittemyer et al., 2005), giraffes (VanderWaal et al., 2014), gorillas (Morrison et al., 2019) and many other primates (Grueter et al., 2012; Grueter & Van Schaik, 2010; Schreier & Swedell, 2009; Stead & Teichroeb, 2019). This social structure has even been detected in vulturine guineafowl, a small-brained bird species (Papageorgiou et al., 2019). In these multi-level societies, individuals have their strongest relationships within their core social unit (or social group) but associate preferentially with certain other units. They therefore represent key species in which the benefits of such a social structure for the use and sharing of space could be investigated.

The genus *Gorilla* is one such example in which relationships between groups form a key part of the overall social structure (Forcina et al., 2019; Mirville et al., 2018a, 2018b; Morrison et al., 2019). Gorilla groups' large home ranges (up to 24 km²) often overlap with those of their neighbours (Bermejo, 2004; Caillaud et al., 2014; Head et al., 2013). Mountain gorilla (*Gorilla beringei beringei*) groups move an average of 500–1,000 m per day, foraging as they move and nesting in a new location each night (Ganas & Robbins, 2005; Grueter et al., 2018; Watts, 1991). Gorilla groups are known to actively avoid one another across much of their ranges, spacing themselves in a manner that reduces home range overlap (Bermejo, 2004; Caillaud et al., 2014; Morrison, Dunn, et al., 2020; Seiler et al., 2017; Watts, 1998). However, neighbouring gorilla groups are still involved in an average of 15 inter-group encounters annually (Caillaud et al., 2014; Mirville et al., 2018b).

Behaviour during these encounters varies considerably, from highly affiliative, with individuals from different groups playing and feeding together, to highly aggressive, involving screaming, biting and pushing (Bermejo, 2004; Mirville et al., 2018b; Robbins & Sawyer, 2007).

Approximately half of mountain gorilla offspring disperse from their natal group around sexual maturity (45% of males and 52% of females; Robbins et al., 2009; Stoinski et al., 2009). New groups form either when a solitary male attracts females or when a group fissions, with at least one adult male and female splitting from a larger group (Nsubuga et al., 2008; Robbins & Robbins, 2005). Fissioned groups then move independently but have been found to show higher rates of affiliative behaviour during inter-group encounters (Mirville et al., 2018b). Interestingly, Mirville et al. (2018b) found no evidence that rates of affiliative behaviour between fissioned groups declined as the amount of time since they had fissioned increased or were influenced by the maternal relatedness of males. The higher rates of affiliation were therefore suggested to be due to the strong relationships formed between both kin and non-kin individuals while residing within the same group. Fissioning in mountain gorillas therefore produces a situation, unusual for a species showing habitual dispersal of both sexes, in which the social preferences of the majority of adult individuals in a group are likely to align, with the potential for stronger social preferences towards groups from whom they previously fissioned.

Due to the potential for peaceful inter-group encounters and extensive home range overlap, gorillas have commonly been described as non-territorial. Despite this, Seiler et al. (2018) identified elements of mountain gorilla ranging behaviour that are usually observed in territorial species: that gorillas avoid core regions of other groups' home ranges and reduce rather than increase their home range size in response to higher population densities. They therefore concluded that mountain gorillas may be intermediate on a gradient between territoriality and non-territoriality. Western lowland gorillas (*G. gorilla gorilla*) have also been found to actively avoid other groups' home ranges and avoid encountering other groups to a greater extent when closer to the centre of those other groups' home ranges (Morrison, Dunn, et al., 2020); another finding consistent with territoriality in gorillas. It was therefore suggested that gorillas may show a more flexible form of territoriality, in which the location, relative to the centre of a group's home range, is one of a number of important factors influencing how groups interact.

We used the long-term data of The Dian Fossey Gorilla Fund to investigate the influence of both social and spatial factors on behaviour during inter-group encounters between 55 pairs of mountain gorilla groups including 11 that had fissioned from each other in the past and 44 that had not. We hypothesized that encounters would be more likely to become aggressive towards the centre of a group's home range due to territorial defence but that social familiarity through either fission history or previous encounters could influence this territorial defence.

2 | MATERIALS AND METHODS

2.1 | Data collection

Between 2003 and 2018, The Dian Fossey Gorilla Fund's Karisoke Research Center monitored between 3 and 11 habituated mountain gorilla (*G. beringei beringei*) groups daily in the Volcanoes National Park (VNP), Rwanda (Figure S2). During this time, 443 encounters were observed between monitored groups. These were classified as either acoustic or visual. During acoustic encounters ($n = 178$), calls or chest beats from one group were heard by researchers following another group which produced an auditory response, but groups did not approach each other. The identity of both groups was confirmed between researchers in the respective groups. Acoustic encounters were not usually recorded over distances >2 km. Encounters were classified as visual if groups approached to within 50 m of each other and made visual contact ($n = 265$). These encounters often began acoustically. The location of each visual encounter was recorded at the point at which groups first made visual contact within 50 m by the research team closest to the encounter. Each gorilla group ($n = 17$) was composed of at least one adult male and one adult female and was observed almost daily for up to 4 hr until the end of the study period or the disintegration of the group.

2.2 | Behaviour during visual encounters

The behaviour recorded during each visual encounter was classified by the presence or absence of affiliative and aggressive behaviour. Affiliative encounters involved the intermingling of both groups and play or affiliative touching between members of different groups. Aggressive encounters involved aggressive physical contact, such as biting, dragging and kicking, and aggressive vocalizations, including screaming and pig-grunting. These categorizations were almost entirely mutually exclusive, with only two encounters showing both affiliative and aggressive behaviour (supplementary methods). Encounters without affiliative or aggressive behaviour consisted primarily of non-physical displays, such as chest-beating, smashing plants or taking a strut-stance. In a small number of cases ($n = 2$), one or both groups avoided each other without displaying. These were excluded from the analysis.

2.3 | Spatial context: Home range location

Ranging data used in this study consisted of ≤ 2 GPS locations for each group per day: the location of a group's nest site and the location of the group at midday. Mountain gorillas move gradually throughout the day between foraging bouts covering small daily travel distances (500–1,000 m) and build new nests in a different location each night (Ganas & Robbins, 2005; Grueter et al., 2018; Vedder, 1984; Watts, 1991). Our sampling method minimized problems of autocorrelation in data points by maximizing the time

between subsequent locations (nest site and midpoint of active period) while avoiding issues of bias due to the lack of any nest-site fidelity (Figure S3; Table S1). However, it remains possible that the use of only these two specific time points could introduce some bias in the home range estimates towards locations utilized more regularly at these times (Supplementary Methods).

Ranging behaviour was investigated using 69,560 GPS locations between 2002 and 2018. A home range specific to each group at each encounter was calculated using all locations for each group in the 365 days prior to the encounter. This was done to account for any gradual shifts in home range location over time (Figure S1). Home ranges were calculated as the area containing 90% of locations (90% kernel density estimate). Core home ranges were calculated as the area containing 50% of locations (50% kernel density estimate; Figure 1). These classifications follow established home range analysis methods used with gorillas (Caillaud et al., 2014; Mirville et al., 2018b; Seiler et al., 2017). Recommendations on the number of data points required to accurately estimate home ranges vary greatly, with a minimum of 10 (Börger et al., 2006), 30–50 (Seaman et al., 1999) and 100 (Girard et al., 2002) locations suggested. We therefore followed a conservative approach only estimating home range locations for encounters when ≥ 90 range locations were available in the 365 days leading up to the encounter, following methods found to be relatively robust to sample size differences in this population (Caillaud et al., 2014). We also excluded encounters involving groups that formed or fissioned within the 6 months prior to the encounter to remove periods when ranging patterns may have been particularly unstable. After this, home ranges were calculated as for all other groups, including all locations

in the 365 days before the encounter. For groups that contained $>50\%$ of the pre-fission group's individuals and the same dominant male we used both pre-fission and post-fission locations for home range estimation (and retained the same group name). Otherwise, fissioned groups were considered as new groups, so only post-fission locations were included, with ≥ 90 locations required for home range estimation. The location of an encounter relative to both groups' home ranges could therefore be estimated for 170 of the 265 total visual encounters. Ranges were calculated using the 'ADEHABITATHR' package (Calenge, 2006), with fixed bandwidth values of 200 to enable comparison across groups and populations (Caillaud et al., 2014).

2.4 | Social context: Fissioning patterns and previous encounters

Seven group fissions occurred within the study period (Figure S2; Table S2). No fissions had taken place for 10 years prior to the study period. Adult female mountain gorillas rarely participate actively in intergroup encounters ($12 \pm 1.4\%$ participation compared to $57 \pm 1.3\%$ in adult males; Mirville et al., 2018a). This difference is even greater for agonistic encounters where $52 \pm 0.2\%$ of adult males participated compared to $1 \pm 0.01\%$ of adult females (Mirville et al., 2018a). We therefore investigated changes in group composition relating to adult males (Supplementary Methods). Fissioning was coded as a binary variable where 1 indicated that the groups had fissioned within the study period and contained only adult males that had been present pre-fission.

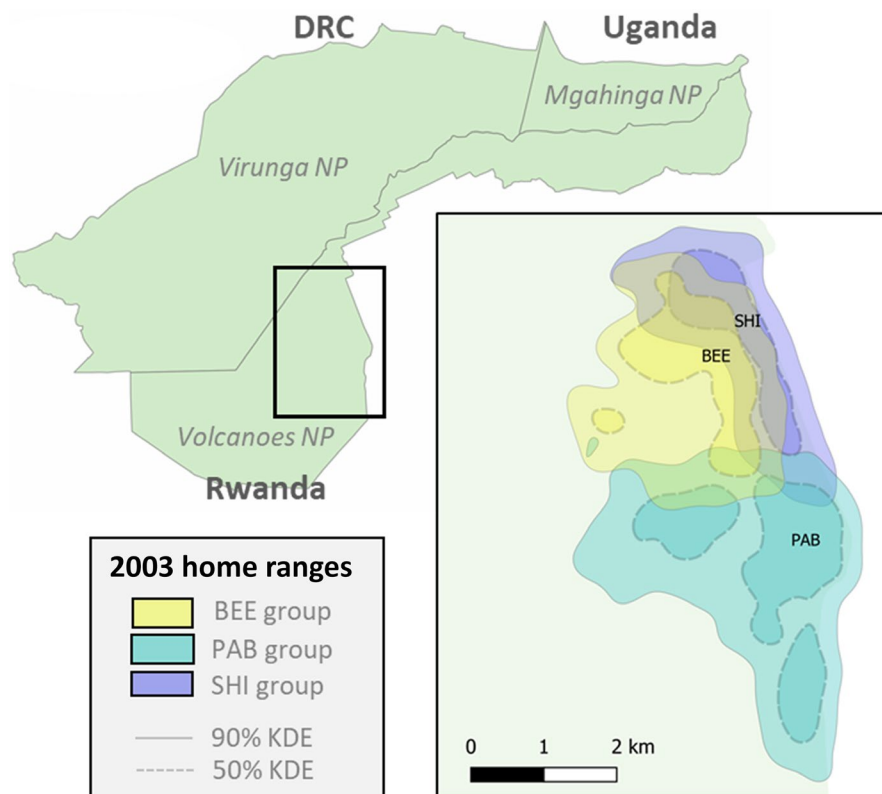


FIGURE 1 Peripheral home range (90% KDE) and core home range (50% KDE) during 2003 for the three groups present. Range location shown within the Volcanoes National Park and the larger Virunga massif consisting of three national parks across three countries

A second social predictor: the familiarity of groups from previous encounters was calculated as the total number of encounters between groups in the 365 days leading up to the encounter of interest. Both auditory and visual encounters were used in this calculation as an estimate of how regularly groups would hear or see one another.

2.5 | Predicting behaviour during encounters

To investigate the influence of social and spatial factors on aggressive and affiliative behaviour during visual encounters, all visual encounters between known groups where the location within both groups' ranges could be estimated were analysed ($n = 170$; Morrison, Hirwa, et al., 2020). This included 56 encounters between groups that had previously fissioned from each other (Figure S2) and 114 encounters between groups that had not.

Binomial generalized linear mixed models (GLMMs) fit by maximum likelihood using the 'LME4' package (Bates et al., 2015) were run to predict behaviour during visual encounters. For each encounter, one group was randomly chosen as the focal group. This approach enabled a simpler comparison across home range locations enabling basic hypotheses about the defence of space to be tested. The location within the focal group's range: core home range (50% KDE), peripheral home range (90% KDE but not 50% KDE) or outside the home range (not within the 90% KDE), was included as a fixed factor. Location was treated as an ordered factor (outside < peripheral < core) and was therefore investigated using orthogonal polynomial contrasts within the GLMM (Christensen, 2011). This enabled the potential for territorial defence following a linear relationship (e.g. linear increase in aggression through the three categories) or following a polynomial relationship (e.g. defence of only the core home range or the entire home range) to be investigated. Group fissions and previous encounters (as described above) were included as predictors to investigate the social context of encounters. The difference in the number of adult males in each group was also included as a fixed factor to account for the relative competitive ability of groups, as primarily only adult males were involved in aggressive encounters (Mirville et al., 2018b). The identity of the focal group was included as a random effect. This model was run twice: once to predict whether aggression occurred during an encounter and once to predict whether affiliation occurred.

Investigating how the social context of visual encounters influenced behaviour differently in different locations could not be done satisfactorily by modelling interactions within the overall model due to the potential for different effects within the intermediate category (peripheral home range) to be masked by similar effects in the core and outside the home range. The dataset was therefore split into three subsets based on their location relative to the focal group (core, peripheral and outside). Aggressive and affiliative behaviour within each location was predicted with binomial GLMMs (six additional models). Both social predictors (fissioning and previous

interactions) were included as fixed factors, along with the difference in number of adult males. The identity of the focal group was included as a random effect.

To investigate the influence of location relative to both groups' home ranges, visual encounters were classified into six location categories (Table S3). The same binomial GLMMs run on the full dataset using three focal group location categories were rerun using these six location categories to predict whether aggression and affiliation occurred (two additional models). The pair of groups involved in the visual encounter was included as a random effect. Due to issues of model convergence, only location and fissioning could be included as predictors in the affiliation model. Due to small sample sizes, modelling how social context influenced behaviour in the six different location categories was not attempted.

The potential for relationships between fissioned groups to change over time was assessed using binomial GLMMs. The presence of affiliative and aggressive behaviour during visual encounters between fissioned groups ($n = 57$) was predicted from location, the difference in number of adult males, the number of encounters in the previous year and the time since the two groups fissioned. The identity of the focal group was included as a random effect.

Cohen's D (Cohen, 1988) was calculated for all models using the 'EMATOOLS' package. This allowed us to assess and compare standardized effect sizes of the variables in each model following the rough rules of thumb proposed by Cohen that values of $d = 0.2, 0.5$ and 0.8 , respectively, defined small, medium and large effect sizes. Cohen's D has been found to over-inflate values in smaller sample sizes (<50). Therefore, a correction factor (Cohen, 1988) was applied to analyses run on sample sizes <50. All models were checked for multicollinearity using variance inflation factors with the 'CAR' package, for which all variables had GVIF values <2, demonstrating an absence of any collinearity issues. All analyses were carried out in R version 3.6.1.

3 | RESULTS

3.1 | Predicting behaviour by location

The likelihood of aggression occurring during inter-group encounters increased towards the centre of groups' home ranges (Table 1). The model also suggested that rates of aggression may decrease with increasing familiarity due to previous encounters, although with a relatively small effect (Cohen's $D = -0.278, p = 0.067$). There was no evidence that familiarity due to groups fissioning from each other or the difference in the number of adult males in each group influenced patterns of aggression overall. Despite a small decrease in affiliation towards the centre of groups' ranges (Cohen's $D = -0.230$, Figure 2b), only fissioning was a significant predictor of affiliation overall, with affiliation considerably more likely between previously fissioned groups (Table 1). There was no evidence that affiliation declined, or aggression increased between previously fissioned groups over time (Table S4).

TABLE 1 Predicting aggressive and affiliative behaviour during inter-group encounters using binomial GLMMs. Location.L and Location.Q represent the linear and quadratic components of location, respectively, when moving from outside the home range to the core of the home range. *p*-values in bold indicate significance at $p < 0.05$

	Aggression				Affiliation			
	Est ± SE	Cohen's <i>D</i>	Z	<i>p</i>	Est ± SE	Cohen's <i>D</i>	Z	<i>p</i>
Intercept	-0.583 ± 0.317	—	-1.841	0.066	-2.352 ± 0.534	—	-4.401	<0.001
Location.L	0.966 ± 0.446	0.340	2.169	0.030	-0.700 ± 0.516	-0.230	-1.357	0.175
Location.Q	-0.332 ± 0.317	-0.133	-1.050	0.294	-0.215 ± 0.375	-0.062	-0.573	0.567
Adult males	0.080 ± 0.129	0.091	0.624	0.533	-0.239 ± 0.225	-0.145	-1.062	0.288
Fissioned	-0.442 ± 0.383	-0.171	-1.154	0.248	2.078 ± 0.480	0.801	4.331	<0.001
Previous encounters	-0.167 ± 0.091	-0.278	-1.834	0.067	0.118 ± 0.103	0.198	1.142	0.253

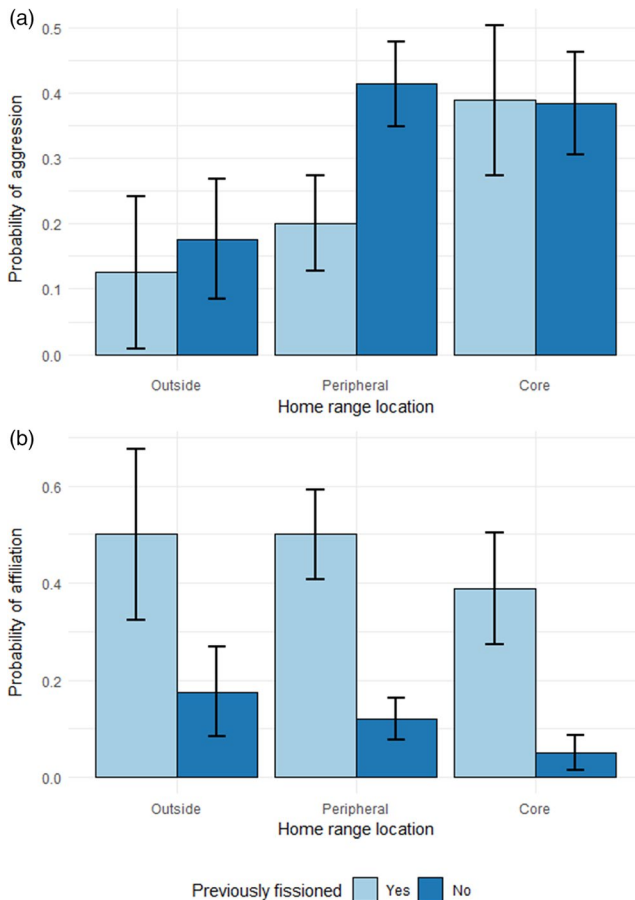


FIGURE 2 The probability of (a) aggression and (b) affiliation during encounters between groups that had previously fissioned and those that had not, with location within the focal group's home range. Error bars indicate standard deviation

3.2 | Social predictors of aggression and affiliation vary with location

Aggression was most common during encounters within the core of a gorilla group's range (Figure 2a). The likelihood of aggression within the core declined with increased familiarity between groups due to previous encounters (Table 2). However, there was no evidence of

decreased aggression between groups that had previously fissioned (Figure 2a; Table 2). A very different pattern was observed within the peripheral home range where the likelihood of aggression was roughly halved in groups that had fissioned, relative to those that had not (Figure 2a; Table 2; Cohen's $D = -0.447$, $p = 0.047$). Outside the home range, levels of aggression were universally low although small sample sizes in this category meant that models lacked the power to detect small effects with significance.

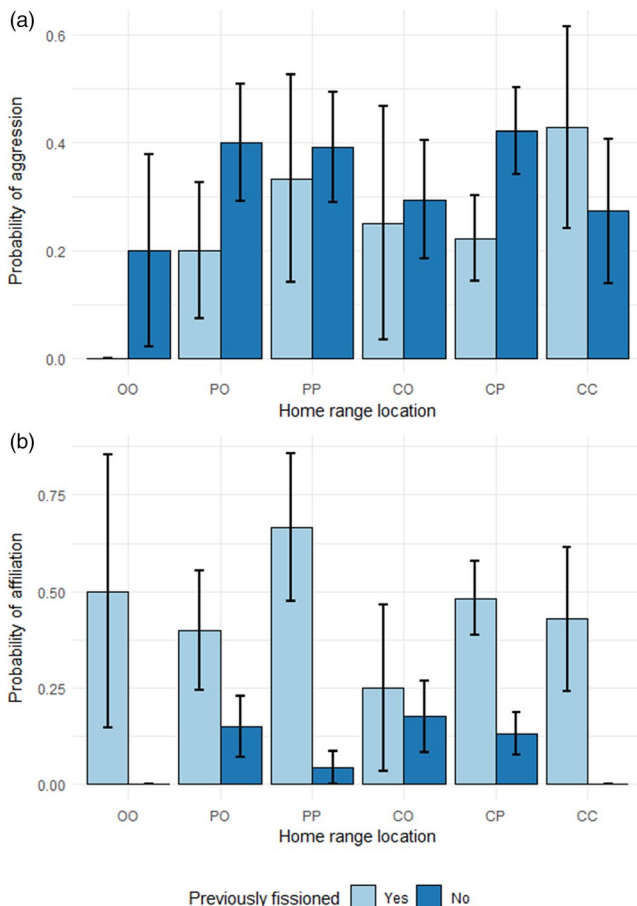
Fissioning was the only significant predictor of affiliative behaviour, with a higher probability of affiliation between fissioned groups in both the core and the peripheries of groups' home ranges (Table 2). Outside the home range, fissioning was no longer a significant predictor. This may, in part, be due to a reduction in power with a smaller sample size. However, the effect size of fissioning was also reduced outside the home range, suggesting that this element of group familiarity may become less important outside the home range with higher rates of affiliation all round (Figure 2b). The largest effect outside the home range was from previous encounters, with higher rates of affiliation between groups that more regularly encountered each other. Despite the large size of this effect (Cohen's $D = 0.978$), it was non-significant ($p = 0.126$), suggesting that the small sample size of encounters outside groups' home ranges limited our ability to predict patterns of behaviour.

3.3 | Predicting behaviour by location relative to both groups

As behaviour during an inter-group encounter is likely to be influenced by both groups, behaviour was also investigated relative to the location of both groups' home ranges. When both locations were accounted for there were no significant predictors of aggression (Table S5). The highest probability of aggression between fissioned groups was found when both groups were within their core home range (Figure 3a). This was also the only location category in which fissioned groups were more likely to be aggressive to each other than non-fissioned groups. The lowest probability of aggression for both fissioned and non-fissioned groups was when both groups were outside their home range. The only predictor with a possible effect

TABLE 2 Predicting aggressive and affiliative behaviour during inter-group encounters using binomial GLMM in differing home range locations (Core home range, peripheral home range and outside the home range). *p*-values in bold indicate significance at $p < 0.05$

	Aggression				Affiliation			
	Est ± SE	Cohen's D	Z	<i>p</i>	Est ± SE	Cohen's D	Z	<i>p</i>
Core (<i>n</i> = 57)								
Intercept	0.137 ± 0.532	–	0.258	0.797	–3.289 ± 1.006	–	–3.269	0.001
Adult males	0.020 ± 0.224	0.018	0.090	0.929	–0.530 ± 0.504	–0.284	–1.051	0.293
Fissioned	0.541 ± 0.689	0.229	0.786	0.432	2.477 ± 1.065	0.777	2.326	0.020
Previous encounters	–0.340 ± 0.166	–0.585	–2.047	0.041	0.340 ± 0.212	0.546	1.601	0.109
Peripheral (<i>n</i> = 88)								
Intercept	–0.528 ± 0.433	–	–1.219	0.223	–1.573 ± 0.729	–	–2.157	0.031
Adult males	0.194 ± 0.175	0.247	1.108	0.268	–0.450 ± 0.319	–0.288	–1.408	0.159
Fissioned	–1.078 ± 0.542	–0.447	–1.989	0.047	2.438 ± 0.693	0.920	3.519	<0.001
Previous encounters	–0.054 ± 0.120	–0.097	–0.452	0.651	–0.095 ± 0.154	–0.146	–0.619	0.536
Outside (<i>n</i> = 25)								
Intercept	0.169 ± 1.458	–	0.116	0.908	–2.754 ± 1.116	–	–2.468	0.014
Adult males	–1.242 ± 1.128	–0.402	–0.101	0.271	0.526 ± 0.567	0.372	0.929	0.353
Fissioned	–1.655 ± 2.163	–0.092	–0.765	0.444	1.285 ± 1.305	0.418	0.985	0.325
Previous encounters	–1.071 ± 0.985	–0.354	–1.087	0.277	0.556 ± 0.364	0.978	1.530	0.126

**FIGURE 3** The probability of (a) aggression and (b) affiliation during an encounter between groups that had previously fissioned from each other and those that had not, by location relative to both groups' home ranges (O: outside the home range, P: peripheral home range, C: core home range). Error bars indicate standard deviation

was the number of previous encounters with a small decrease in aggression between groups that encountered each other more often (Cohen's $D = -0.254$, $p = 0.093$).

No location categories showed a significantly different probability of affiliative behaviour compared to when both groups were outside their respective home ranges (Table S5). Fission history remained a strong predictor of affiliation overall. The probability of affiliation was higher in fissioned groups across all location categories except when one group was within their core and another was outside their home range, where standard deviation error bars overlapped (Figure 3b). This category had the lowest probability of affiliation between fissioned groups.

4 | DISCUSSION

Our findings suggest that behaviour during encounters between gorilla groups is influenced by both their social and spatial context. The space-associated aggression detected in this gorilla population suggests the presence of territorial defence, with the probability of aggression highest in the core of the home range and decreasing towards the peripheries. However, this effect appears to be relatively weak. These findings support the hypothesis proposed in Morrison, Dunn, et al. (2020) that gorillas show a form of territoriality where groups do not have hard territory borders, but rather, show location-dependent defence of space. Combined with the findings of Seiler et al. (2018), it suggests that weak territoriality may be the norm in gorillas, where location is one of many factors such as familiarity (Mirville et al., 2018b) and mating competition (Robbins & Sawyer, 2007) which influence movement patterns and behaviour during inter-group encounters. This is a relatively

unusual finding, given the widespread nature of most gorilla food resources and the lack of increased aggression in areas with limited food resources (Mirville et al., 2018b). Future research on the distribution and seasonal availability of resources within home ranges could provide further clarity on these patterns of territorial defence.

When encounter location relative to both groups' home ranges was investigated, the effect of location was weak and insignificant, with no clear pattern of territorial defence overall. This may, in part, be due to inadequate sample sizes to detect the relatively small effect of location when split across the larger number of categories. It is also less clear what the expected pattern of territorial defence would be in this context. Will gorilla groups defend their core more strongly against a group with an overlapping core range that they more frequently encounter, or a group from further away that has travelled outside their home range? Are encounters more likely to escalate into aggression when groups are similarly matched in their use of a given area or when one group uses an area more often than another? A greater amount of data is required to satisfactorily investigate these issues.

When analysing the data in relation to a single focal group, groups showed less aggression towards groups that they had previously fissioned from within the peripheries of their home range, but not the core of that home range. This suggests that the strong social relationships formed between individuals within the same group may enable them to access regions of neighbouring groups' home ranges with a reduced risk of aggression if groups remain in close proximity following fissioning. These patterns show potential parallels with human hunter-gatherer populations in which inter-territorial visits are often restricted to kin or those with close relationships that may be sustained over long periods or even generations (Cashdan, 1983). Considerable effort is thought to be spent strengthening such inter-group relations in these human populations to ensure hospitality is reciprocated (Axelrod & Hamilton, 1981; Cashdan, 1983). The higher levels of affiliative behaviour we detected between fissioned mountain gorilla groups could serve a similar function, enabling reciprocal territory access or other potential benefits.

In other animal societies, preferential relationships between groups have been proposed to provide a variety of benefits through either kin selection or reciprocal altruism such as the defence of females (Xiang et al., 2014), increased foraging efficiency (Morrison et al., 2019), knowledge transfer (de Silva & Wittemyer, 2012; Wittemyer et al., 2005) and predation avoidance (Matsuda et al., 2010; Whitehead et al., 2012). However, the potential benefits of these relationships for improving access to neighbouring home ranges have not been studied in these societies. Such benefits might only be present in populations with both inter-group social preferences and some level of territoriality, which may be a rare combination if aggressive defence of space impedes the formation of inter-group relationships, or vice versa. However, it is also possible that both territoriality and inter-group social preferences are present in other species but that their simultaneous presence might prevent the detection of either or both behaviours.

In African elephants, preferentially associating groups are thought to be those that have previously fissioned from each other, with associations persisting for decades, even after the original group members have died (Archie et al., 2006; Wittemyer et al., 2005). Similar patterns are also suggested in matrilineal, multi-level sperm whale and killer whale societies (Bigg et al., 1990; Konrad et al., 2018). In mountain gorillas, Mirville et al. (2018b) demonstrated that affiliative relationships between fissioned groups were maintained over a 5-year period. Our results demonstrating no significant decline in affiliative behaviour between fissioned groups over 10 years (Table S4) build on this further. They suggest that, similarly to human, elephant and whale societies, these affiliative relationships between fissioned groups are maintained over many years. In mountain gorillas, the extended periods of social contact provided by common membership of a group (prior to fission) may be key in developing the strong relationships required for affiliative inter-group encounters and access to areas within neighbour's home ranges. These fissioned groups are also likely to be more closely related and it is extremely difficult to disentangle the effect of kinship or perceived kinship, and common group membership on these social preferences (Mirville et al., 2018a, 2018b). Further study is also required to better understand the individual relationships between those in different groups, how these shape the behaviour of the groups overall and how this can change over time.

Despite the social preferences between fissioned groups, higher rates of aggression were observed within core home ranges regardless of fission history. Instead, aggression in this region was lower between groups that encountered each other more often. In the core, defence may be the common response but the dominance of one group over another may already be established in groups that regularly interact, causing one group to retreat before the encounter becomes aggressive (Maynard Smith, 1974; Mirville et al., 2018a). This familiarity from previous interactions may differ from that based on previous presence within the same group, as it is based on more recent interactions with potential competitors, rather than the more cooperative long-term experience of co-residence within the same group.

When analysing aggression in relation to both groups' home ranges, fissioned groups were only more aggressive than non-fissioned groups when both groups were within their core home range (although not significantly). Aggression in this context may provide an important mechanism by which groups adjust their home ranges after fissioning, leading to a reduction in home range overlap and associated competition. In contrast, non-fissioned groups had the highest levels of aggression when at least one group was within their peripheral home range. For groups that have not fissioned from each other, the peripheral home range may be where the majority of territorial disputes occur.

Outside the home range, when analysing the data in relation to a single focal group, neither social predictor influenced aggression, which was universally low. This was also the only location in which there was no significant difference in affiliative behaviour between fissioned and non-fissioned groups. While this may, in part, be due to a lack of power, the effect size of fissioning was also at its lowest,

suggesting that a relaxation of territorial defence outside the home range may enable more affiliative encounters even between unfamiliar groups. These areas may therefore function similarly to public spaces in modern and particularly urban human populations where individual ownership of space does not apply.

Overall, most of the predictors of behaviour during encounters that we identified were relatively weak and evidence for territorial defence across models was mixed. One possible reason is that in this complex social system, many factors may influence these behaviours such that any single predictor might have only a small effect. Combined with the relative rarity of inter-group encounters, this may limit our ability to identify clear predictors of behaviour. A further difficulty is that in many instances (40.2% of encounters) gorilla groups interacted acoustically but did not approach each other. Most visual encounters began acoustically before groups approached, suggesting that for the most part, when visual encounters occur, groups are actively deciding to approach rather than meeting unexpectedly. If gorilla home ranges are aggressively defended, groups may avoid encountering their neighbours more when within their neighbours' home ranges. Indeed, there is evidence supporting this in western lowland gorillas (Morrison, Dunn, et al., 2020). The more effective territorial defence becomes at preventing neighbour intrusions, the harder it may become to detect from aggression. While our analyses of aggression relative to the location of a single focal group suggest the presence of territorial defence, no clear pattern is observed when location is investigated relative to both interacting groups' home ranges. Our analyses suggest that different social factors may come into play in the decision to defend different home range regions but that we are limited in our ability to determine precisely how with the currently available data. However, this may become more feasible in the coming years, if the mountain gorilla population continues to grow and inter-group encounters continue to increase in frequency.

5 | CONCLUSIONS

Our findings suggest that gorillas show weak territoriality and that, as in humans, this territoriality is sensitive to differences in social relationships (Cashdan, 1983). The presence of social relationships not only within groups but also between groups is a key component in the evolution of humanity's complex society and large-scale cooperation, and something that we appear to share with gorillas as well as many other species. We find that such social relationships in gorillas enable the access of peripheral but not core areas of neighbouring groups' home ranges with a reduced risk of aggression, and therefore that the social component of territoriality is not a phenomenon specific to human culture (Cashdan, 1983). Instead, we suggest that a reduction in territorial aggression between preferred neighbouring groups in certain regions may represent an important benefit to the evolution of long-term, affiliative inter-group relationships, with the potential to have influenced the evolution of complex multi-level societies across numerous species.

ACKNOWLEDGEMENTS

We are grateful to the Rwandan Development Board (RDB) for their long-term support of the Karisoke Research Center and thank all the Karisoke field staff for their work. We thank Peter Walsh and Magdalena Bermejo for discussion that inspired this project. We are grateful to Lauren Brent and researchers at the Centre for Research on Animal Behaviour at the University of Exeter for hosting R.E.M. while parts of this work were carried out and providing insightful discussion.

AUTHORS' CONTRIBUTIONS

R.E.M. conceived the project with feedback from T.S.S. and W.E.; Data collection and cleaning was carried out and overseen by J.P.H., J.P.S.M., T.S.S., V.V. and W.E.; Data were compiled by V.V. and analysis was carried out by R.E.M. with advice from T.S.S. and W.E.; R.E.M. wrote the manuscript with feedback from all authors.

DATA AVAILABILITY STATEMENT

Inter-group encounter data analysed in the models are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.hmgqnk9f2> (Morrison, Hirwa, et al., 2020).

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SUPPORTING INFORMATION

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How to cite this article: Morrison RE, Hirwa JP, Mucyo JPS, Stoinski TS, Vecellio V, Eckardt W. Inter-group relationships influence territorial defence in mountain gorillas. *J Anim Ecol*. 2020;00:1–11. <https://doi.org/10.1111/1365-2656.13355>