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Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys

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In social species, fighting in intergroup conflicts is one of the riskiest cooperative activities group members engage in, particularly for individuals of the smaller sex. In a number of species, female group members are significantly smaller than males, so the costs associated with intergroup aggression outweigh the potential benefits and females avoid participating. Studies conducted on species in which females are active participants have consistently found that they fight to defend access to food resources and that high-ranking females tend to be more active than low-rankers. However, additional factors may modulate the costs and benefits of participation, creating differences between individuals and variability within individuals over time. In this study, we investigated costs and benefits that potentially affect female vervet monkey, *Chlorocebus aethiops pygerythrus*, participation in intergroup conflicts. We observed the participation of 35 females in three groups, during 115 intergroup conflicts. Our findings suggest that female vervet monkeys defend access to valuable food resources, as well as to areas that are intensely used in the long term; however, rank also influenced female participation indicating that the potential benefits gained from resource defence vary with one's priority of access to these resources. We found that females were more likely to participate aggressively when they did not have an infant, and when they received more male support throughout the intergroup conflict, suggesting these factors influence the perceived risk, or costs, of intergroup aggression. Because we observed considerable temporal variability in both the proportion of female group members with infants and the number and identity of male group members (i.e. amount of male support provided), the relative fighting ability of neighbouring groups will inevitably fluctuate. Thus, our findings may help explain the lack of stable intergroup dominance relationships observed in many studies of intergroup conflict.
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Intergroup conflicts are one of the riskiest cooperative acts in which social groups engage as they can potentially result in the injury or even death of participants (Cant, Otali, & Mwanguhya, 2002; Cheney & Seyfarth, 1987; Fashing, 2001; Goodall, 1986; Hölldobler & Lumsden, 1980; Mech, 1994; Mills, 1983; Mosser & Packer, 2009). Even when the risk of injury is relatively low, intergroup conflicts can last for long periods and involve vigorous activities such as long chases (Sillero-Zubiri & Macdonald, 1998; Sorato, Gullett, Creasey, Griffith, & Russell, 2015; Wich & Sterck, 2007) and impose significant opportunity costs on participants (Mares, Young, & Clutton-Brock, 2012). Individual group members must each weigh these costs against potential benefits and decide whether to participate or defect from cooperative intergroup aggression. Because male fitness is primarily limited by access to receptive females (Trivers, 1972), it is thought that males mainly participate in intergroup conflicts to defend access to mates (Cooper, Aureli, & Singh, 2004; Fashing, 2001; Kitchen & Cheney, 2004; Koch, Signer, Kappeler, & Fichtel, 2016; Majolo, Ventura, & Koyama, 2005; Payne, Lawes, & Henzi, 2003; Zhao & Tan, 2010). Conversely, female fitness is most limited by access to the resources required to produce and raise offspring (Trivers, 1972) and, therefore, females are thought to participate in intergroup conflicts to defend access to resources such as territory, food, shelter and/or water (Boydston, Morelli, & Holekamp, 2001; Kinnaird, 1992; Nunn & Deaner, 2004; Zhao & Tan, 2010). A number of other factors probably modify these basic costs and benefits; however, few studies have specifically investigated how females decide whether to defect or participate in intergroup conflicts (Reviewed in Kitchen & Beehner, 2007). In a number of social species, females are significantly smaller than males, making the risk of being injured

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during intergroup conflicts so great that they may not participate at all (Willems, Hellriegel, & van Schaik, 2013). Female motivations for intergroup aggression are thus often not expressed and cannot be studied. Even in species in which females do participate in intergroup conflicts, they are often less active than males (reviewed in Cheney, 1987; Koch et al., 2016), making it difficult to obtain the data necessary to effectively examine the factors that influence intra- and interindividual variability in participation.

Although there is a risk of injury when two groups fight over contested resources, the level of risk may differ between groups and between individual group members, and may depend on the behaviour of both fellow and opposing group members. An individual's reproductive status, age, size and fighting ability relative to the participants from the opposing group can all affect how risky an intergroup conflict is perceived to be (Kitchen & Beehner, 2007). For females, the level of sexual dimorphism and their reproductive status are likely to have a significant influence on risk perception. In species in which sexual dimorphism exists, but is moderate enough that females are willing to participate in intergroup conflicts, females may perceive the risk of injury to be higher if males from the opposing group are likely to participate aggressively. Mothers have invested significant time and resources into each of their offspring, and infants are particularly vulnerable group members (Arseneau, Taucher, Van Schaik, & Willems, 2015; Cheney & Seyfarth, 1987; Hrdy, 1974; Packer & Pusey, 1983); thus, mothers could be expected to be risk averse during intergroup conflicts (van Schaik, 1996).

In social species, competitive ability is typically thought to be a product of group size (Cheney, 1987; Mosser & Packer, 2009; Williams, Oehlert, Carlis, & Pusey, 2004) and, therefore, individuals in numerically inferior groups may be at a greater risk of injury (Hölldobler, 1981; Mosser & Packer, 2009; Sillero-Zubiri & Macdonald, 1998). However, whenever cooperative intergroup aggression is not a collective but a joint action by a subset of group members only (Willems, Arseneau, Schleuning, & van Schaik, 2015), the relative number of active participants, rather than relative total group size, may determine the outcome of intergroup conflicts (Zhao & Tan, 2010) and the perceived risk of intergroup aggression. Furthermore, the identity of active group members may also influence individual decisions, with larger or more experienced fighters being more valued allies (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015). For example, it is possible that for females, having support from larger male group members may mitigate the perceived risk of participation in intergroup conflicts. Individuals may thus make instantaneous participation decisions based on the current activity of group members.

Females are predicted to fight in intergroup conflicts for access to limiting resources when these are patchily distributed so as to be defensible (van Schaik, 1989; Sterck, Watts, & van Schaik, 1997; Wrangham, 1980). However, when females reside in a stable home range, areas that consistently produce defensible resource may also be valuable and females may defend these spaces, even when current resource availability is low. How females value space and food is likely to vary from species to species, depending on their diets, their local habitat and the intensity of intergroup competition. The benefits gained from defending contested resources may also vary between individual group members, with high-ranking females, who have priority of access, experiencing the greatest incentive to participate in intergroup conflicts (Nunn & Deaner, 2004; Payne et al., 2003; van Schaik, 1989).

In this study, we investigated the costs and benefits of female intergroup aggression in vervet monkeys, *Chlorocebus aethiops pygerythrus*. Vervet monkeys live in multimale, multifemale groups and, although females are smaller than males, the level of sexual dimorphism is modest enough that females are willing to participate aggressively during intergroup conflicts (Cheney, 1981). Females fight with and without male support, and can even physically attack members of opposing groups (Cheney & Seyfarth, 1987). Although females direct intergroup aggression towards both males and females (Cheney, 1981), their tendency to form a coalition when attacking males during intragroup conflicts (Arseneau-Robar et al., 2016) suggests that targeting males carries a relatively high risk of injury if the male retaliates. Therefore, the support of group members, in particular larger male group members, may mitigate the perceived risk of participation in intergroup conflicts. Vervet monkeys are a particularly suitable species for investigating intra- and interindividual variability in participation, as usually only a handful of group members are active in a given intergroup conflict, individual participation is highly variable and larger groups are not guaranteed to win (Arseneau et al., 2015; Willems et al., 2015). As a result, individual decisions to defect or participate may have real consequences for the outcome of intergroup conflicts, subsequent resource access and potentially the fitness of group members (Cheney & Seyfarth, 1987; Lee & Hauser, 1998).

The goal of this study was to examine the factors that influence female participation in intergroup conflicts, and thereby gain a better understanding of the costs and benefits of participation versus defection from cooperative intergroup aggression. We considered three factors that could potentially modulate the risk of injury, and thus the costs, associated with intergroup aggression: female reproductive status, relative group size and the amount of male support. We hypothesized that females with vulnerable infants would be more averse to the risks posed by intergroup conflicts and, therefore, we expected that these mothers would avoid participating in intergroup aggression. We also expected that having support from male group members would mitigate the perceived risk of injury and, therefore, that females would be more likely to participate when they had greater support from their larger male group members. Because individual participation is highly variable and only a handful of group members typically participate in a given intergroup conflict, we did not expect relative total group size to have a strong effect on the perceived risk of intergroup conflicts, and therefore we predicted this variable would have a minimal impact on the likelihood of females exhibiting intergroup aggression. Given the prevalence of evidence for female food defence in the literature (reviewed in Kitchen & Beehner, 2007), we predicted that females would be more likely to participate in intergroup conflicts that occurred in the season when, and in areas of their home range where, food availability was greatest. However, because females are the philopatric sex, it is also possible that the long-term value of the intergroup conflict location (i.e. areas that are consistently used at a high intensity) could influence female participation. We further predicted that high-ranking females, who have priority of access to food resources and therefore receive a disproportionate amount of the benefits of cooperative intergroup aggression, would be more likely to participate in intergroup conflicts.

METHODS

Study Site, Subjects and Data Collection

Data were collected on three habituated groups of vervet monkeys at the Mawana Game Reserve (28°00′S, 31°12′E), KwaZulu-Natal, South Africa, between January 2012 and February 2014. Three seasons are important in this species/population: the birth season, the summer season and the mating season (Arseneau et al., 2015). The birth season was indexed by the number of dependent infants (less than 3 months old) in the group; the first birth typically occurred in early October and the number of infants in the group peaked in late November to early December. Seasonal

habitat productivity was indexed by the average normalized difference vegetation index (NDVI) for each month, and the summer season, when NDVI values were highest, typically peaked between December and April. The mating season typically ran from February or March until August.

The study groups consisted of 30–56 individuals, 6–14 of which were adult females. All individuals were individually recognized, as were most of the adults in four neighbouring and frequently encountered groups. Males were deemed adults when they dispersed from their natal group, while females were considered adults when they gave birth to their first infant. Individual females were classified as having an infant if they had an offspring that was less than a year old. We used the 1-year designation because although females probably perceive infants to be most vulnerable when they are very young and still clinging, many of the observed attacks occurred when the infants were becoming more independent. It appears that this is when infants were more likely to stray too far away from their mothers to be quickly collected, and had also not yet learned where to flee to, if an intergroup conflict erupted. Infants left behind as their group fled the contested location were always attacked and in one case, the infant subsequently died. By the start of the next birth season (i.e. when infants are a year old) they seem to have learned in which direction to flee when intergroup conflicts occur in the various areas of their home range.

Groups were followed for at least 2 full-day follows a week, for a total of >11 000 observation hours over the study period. During follow days, 10 min group scans (Altmann, 1974) were conducted every half hour, during which observers recorded the location of the group centre with a handheld GPS unit (Garmin GPSMAP64, Garmin Ltd., Schaffhausen, Switzerland), and the behaviour of as many group members as possible. During follow days, intragroup social interactions were also recorded as all-occurrence data (Altmann, 1974), and aggression and displacements were used to determine the dominance hierarchy. We recalculated the dominance hierarchy each year so that female group members who had had their first infant (i.e. were deemed adults) could also be included. Hierarchies were estimated using both de Vries h' and the directional consistency index (DCI) because the de Vries method cannot determine a linear relationship when there are only a few individuals (i.e. fewer than six), or provides inaccurately low linearity index values when interaction frequencies are low (Appleby, 1983; Archie, Morrison, Foley, Moss, & Alberts, 2006; Isbell & Pruetz, 1998; Isbell & Young, 2002; Koenig, Larney, Lu, & Borries, 2004; Schmid & de Vries, 2013), as was the case for mother–daughter dyads in this population. Both observed h' values and DCI values were significant in all but one case, indicating that female vervets in this population, as is well established for this species (e.g. Struhsaker, 1967), formed linear dominance hierarchies (h' range 0.59–0.89; DCI range 0.96–1). The one exception was in the smallest group ($N = 6$ females), where h' was 0.83 ($P = 0.12$) in the first year of the study period; however, the DCI indicated that the hierarchy was significantly linear. Therefore, we assigned individual females with a numerical value representing their ordinal rank, with '1' being the dominant female.

During follow days, whenever two groups approached within 100 m of each other, observers noted the time and the location, and also began to record the participation of all adult female and adult male group members on an all-occurrence basis (Altmann, 1974). Because the habitat at the study site is fairly open, and because individuals participating in intergroup conflicts tended to do so on the ground, it was possible to follow the front-line of the intergroup conflict and collect detailed behavioural data. Intergroup encounters were considered intergroup conflicts when one or more individuals from either group directed aggression towards the opposing group. Aggressive behaviours could be directed towards the opposing group as a whole (e.g. running at the group or making aggressive displays and/or vocalizations while in close proximity) or target specific individuals (e.g. chasing or biting). For each aggressive participation event, we recorded the identity of active individuals, behaviour(s) exhibited and the identity of the target individuals (or their sex and age class when their identity was unknown). Individuals were deemed to have initiated the intergroup conflict if they were participants in the first aggressive event of the intergroup conflict. Note that only individuals from the group who exhibited intergroup aggression first could be classified as initiating the intergroup conflict.

Delineating Mapping Units

Because the Mawana Game Reserve is an amalgamation of smaller farms that have been allowed to regenerate, and these farms varied in their use of the land, the study site is composed of fairly discrete habitat patches. Some areas have relatively tall trees and dense vegetation cover, others are open woodlands and others are regenerating fields that contain dense thickets of early successional trees and shrubs. The boundaries of these habitat patches tend to be clear and identifiable by abrupt changes in vegetation density and composition. The landscape is further fragmented by natural (e.g. rivers) and man-made (e.g. roads and fence-lines) linear features, creating a mosaic of discrete areas. The vervet monkeys in the study population also treated the landscape as being heterogeneous as group members spread out within one area to forage, rest and socialize. Then, when moving to the next area, group members typically grouped together to travel as a cohesive unit, and then again spread out to forage, rest and socialize once in the next habitat patch. Furthermore, when an intergroup conflict occurred, the winning group typically pursued the losing group until its members had left the contested area (but did not pursue them past the boundary of the distinct habitat patch). Therefore, we delineated the study area into mapping units which represented these discrete habitat patches, using a satellite image of the study site, the changes in the density and composition of the vegetation, linear features and the behaviour of the monkeys themselves (Fig. A1).

Intensity of Use of Mapping Units

Previous studies have shown that the location in which an intergroup conflict occurs can have a significant effect on the participation of individual group members and the outcome of the intergroup conflict (Crofoot & Gilby, 2012; Crofoot, Gilby, Wikelski, & Kays, 2008; Furrer, Kyabulima, Willems, Cant, & Manser, 2011; Markham, Alberts, & Altmann, 2012; Roth & Cords, 2016). In accounting for this potentially important location effect, we did not use the distance to home range centre (Crofoot & Gilby, 2012) because in this population, study groups did not have a single, centrally located core area. Instead, all study groups had multiple mapping units that were intensely used, which could occur either near the centre or at the edge of the home range. Therefore, we determined which mapping units were, and were not, consistently used at a high intensity over the long term (i.e. in both years of the study period). We used locations collected during group scans to estimate utilization distributions for each group, each year (i.e. January 2012 to January 2013, and February 2013 to February 2014), using the Brownian bridge movement model (Horne, Garton, Krone, & Lewis, 2007) as implemented by Buchin, Sijben, Arseneau, and Willems (2012) and Buchin et al. (2015). We calculated the average intensity of use for all cells within each mapping unit for the first and second year of the study period. All groups had one or two mapping units that were consistently used at a high intensity (i.e. units that had a high long-term value), while most

mapping units within each group's home range were not consistently used at a high intensity (>60% as often as the most intensely used mapping unit).

Habitat Productivity and Relative Food Availability

We examined variability in habitat productivity both seasonally and spatially. Seasonal habitat productivity was indexed by monthly NDVI values from the MODIS MCD43A4 data set (version 5, processed by NASA's LP DAAC (NASA Land Processes Distributed Active Archive Center (LP DAAC), 2014) and redistributed by WAMIS at: http://wamis.meraka.org/za/). The NDVI is a well-established proxy of the amount and vigour of green vegetation which correlates with the availability of food and shelter in vervet monkeys (Willems, Barton, & Hill, 2009). High NDVI values were observed in the summer months (December to April), which is the period when almost all tree species important in the diet of the vervet monkeys in this population produce fruits. Conversely, outside the summer season, the monkeys had a more varied diet, foraging for insects, eating tree sap and sifting through the soil to find *Acacia* seeds that had dropped to the ground as the pods dried and cracked open.

While we used the intensity of use of each mapping unit to represent its long-term (i.e. annual) value to each group, the relative availability of food was used to represent the short-term (i.e. current monthly) value of each mapping unit. Within each month, we accounted for the spatial variability in food resources by determining the relative calories available from fruits in each mapping unit within each home range. Throughout the study period we conducted monthly phenology sampling, estimating the number of fruits per tree on 10 trees of each of the nine species most commonly consumed by vervet monkeys at the field site ($\geq$75% of their diet, based on the fruits consumed during group scans). We determined the spatial distribution of these species by overlaying the study area with a 100 m by 100 m grid and counting the trees of each species within each grid cell. We selected the four species that were most important in the diet of the study groups (ca. 40% of their diet) and were also heterogeneously distributed. Using the caloric values of these fruits (Barrett, 2009; El Ayadi, Msanda, Baniaameur, & El Mousadik, 2012; Feedipedia, 2015) and the average number of fruits per tree observed during phenology sampling, we estimated the total calories available per grid cell, for each month of the study period. The calories per grid cell were averaged within each mapping unit, and we calculated the relative value of each mapping unit within each group's home range in a given month by dividing the average caloric value of each mapping unit by the average caloric value of the best unit available to that group, that month. Because we calculated the relative food availability of mapping units, we only included the tree species that were heterogeneously distributed, and, therefore, whose availability varied between mapping units.

Statistical Analyses

We built two generalized linear mixed models (GLMMs). The first model tested which factors influenced whether individual females initiated intergroup conflicts, while the second model tested which factors influenced their propensity to participate throughout the intergroup conflicts. Predictor variables included female rank and whether they had an infant, the three seasons (i.e. birth, summer and mating seasons), and the two location factors: the long-term intensity of use (low versus high) of the mapping unit the intergroup encounter occurred in and the current availability of food in the contested mapping unit, relative to the rest of the home range. Additionally, because previous studies have shown that an individual's participation can vary with the relative fighting ability of its group (Heinsohn & Packer, 1995; Kitchen, 2006), we also added relative group size (number of adults and subadults in the focal group minus the number in the opposing group) as a predictor variable. In the second GLMM, in which we investigated female participation in intergroup conflicts, we also included the amount of male support that was given during the intergroup conflict as a predictor variable. The amount of male support was calculated as the proportion of aggressive events in the intergroup conflict, in which one or more males participated.

All statistical analyses were conducted in R (version 3.0.3, R Core Team, 2014) using the lme4 (version 1.1-4, Bates, Maechler, Bolker, & Walker, 2015), MuMIn (version 1.10.5, Bartoń, 2014) and compete packages (version 0.1, Curley, 2016). Because the response variable in both GLMMs was binary (i.e. initiate intergroup conflict yes/no, or participate in intergroup conflict yes/no), we set a binomial error structure and logit link function in our models. We included female identity nested within group and intergroup conflict as crossed random effects to account for repeated sampling of individuals over different encounters (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We tested the significance of any interaction term that we thought biologically relevant using a likelihood ratio test (chi-square test statistic), comparing the model with only main effects included to the model with each interaction included (Bolker et al., 2009; Zuur et al., 2009). Only interactions that improved model fit at the significance level of $\alpha = 0.05$ were retained in the final model.

We based our inferences on full models plus important interaction effects rather than using a stepwise procedure (Forstmeier & Schielzeth, 2011), and we did not interpret main effects if the predictor variable featured in a significant interaction effect. The significance of each GLMM was assessed by using a likelihood ratio test to compare the final model to the null model, which only included the intercept and random effects. The total variance explained ($R^2_{GLMM(c)}$) by each GLMM was estimated following the method described by Nakagawa and Schielzeth (2013).

Ethical Note

All data collection protocols were approved by the Ezemvelo KZN Wildlife board in South Africa.

RESULTS

We observed more than 400 intergroup encounters, half of which escalated into an intergroup conflict. We restricted our analyses to a subset of 115 intergroup conflicts in which all independent factors were known. There was a high amount of intra- and interindividual variability in the proportion of intergroup conflicts in which the 35 females in the three study groups participated (Fig. 1). Some females were relatively consistent participants, some were almost never active, but most exhibited considerable annual variability in the proportion of intergroup conflicts in which they participated (Fig. 1). In general, dominant females were frequently active in intergroup conflicts, whereas females who consistently defected from participating in intergroup conflicts tended to be low ranking. Additional variability may be attributed to reproductive status; when considering only those females that experienced annual variability in their reproductive status, we found that females participated in 35% of intergroup conflicts in year(s) that they did not have infants and 23% of intergroup conflicts in year(s) that they did. The proportion of female group members giving birth in a year ranged from 25% to 100%.

In our first analysis, we investigated the factors that influenced the propensity for individual females to escalate intergroup encounters into intergroup conflicts (i.e. participate in the first act of intergroup aggression). We found that high-ranking females were

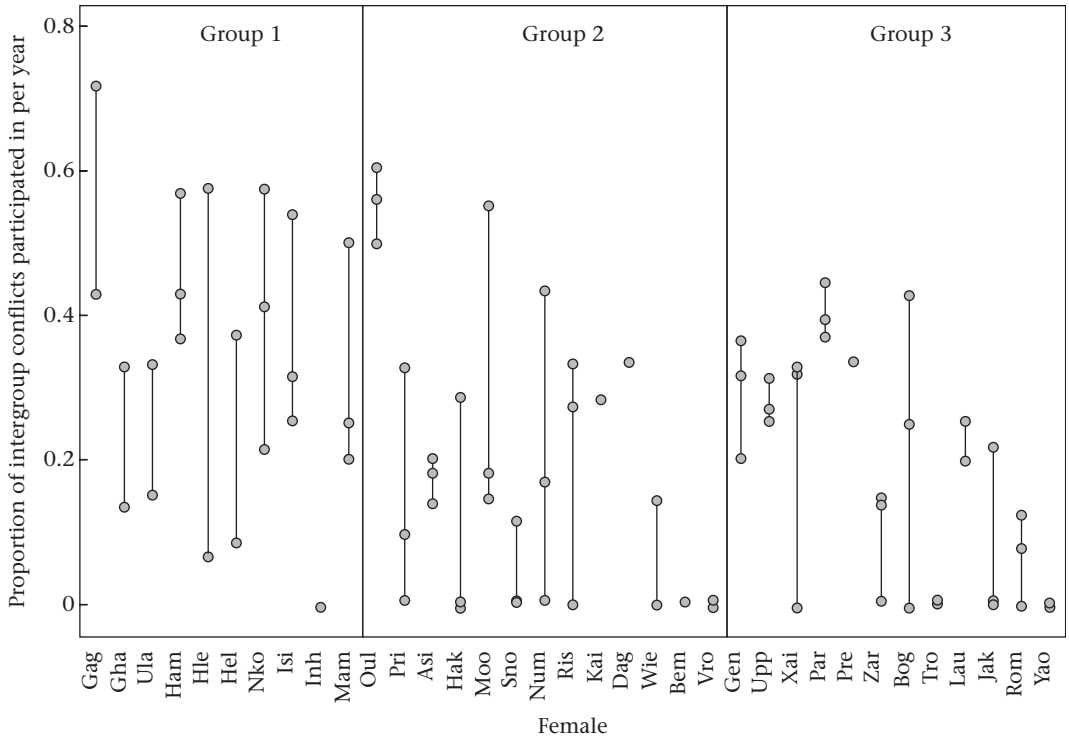

Figure 1. Annual variability in the proportion of intergroup conflicts experienced in which individual females participated. Females are listed in order of descending rank, with the dominant female from each of the three groups listed first. Each dot represents a year of the study period; not all females were present in all years, and some females only reached adulthood in the second or third year of the study period.

more likely to initiate intergroup conflicts than the lower-ranking members of their group (Table 1), and that alpha females were particularly likely to do so; they initiated approximately half of intergroup conflicts they experienced, while the average lower-ranking female only did so in 22% of the intergroup conflicts that they experienced. We also found that females were more likely to initiate intergroup conflicts when the contested location was within one of the mapping units that their group consistently used intensely over the long term (Table 1).

In our second analysis, we investigated which factors influenced female participation throughout escalated intergroup conflicts. In general, females were more active in intergroup conflicts in the summer when high-quality fruits were abundant, and high-ranking females were more active than low-ranking females (Fig. 2a and b, Table 2). However, rank effects were more pronounced when the intergroup conflict took place in mapping units that had high food availability, relative to the rest of the home range (Fig. 2b, Table 2). Rank effects were weaker when intergroup conflicts took place in mapping units with relatively little food available, but females still fought to defend these areas in the summer months when even areas with relatively low food availability contained valuable fruit resources (Fig. 2a, Table 2). We also found that females were more likely to participate in intergroup conflicts that occurred in mapping units that their group used intensely in the long term (Table 2).

Having an infant had a strong negative effect on the propensity of females to participate during intergroup conflicts, indicating that females were significantly less likely to participate in intergroup aggression in years that they gave birth than in years that they did not (Table 2). Conversely, females were more likely to participate aggressively during intergroup conflicts in which male group members provided high levels of support (Table 2).

Table 1
Factors affecting the probability that individual female vervet monkeys participated in the first act of intergroup aggression (i.e. initiated aggressive intergroup conflicts)

Fixed effects	*B*	SE	*z*	*P*
(Intercept)	−3.15	2.34	–	–
Female characteristics				
Rank	**−0.31**	**0.08**	**−4.04**	**<0.001**
Had an infant that year	−0.41	0.56	−0.74	0.458
Seasonal factors				
Birth season	0.11	0.18	0.59	0.554
Seasonal habitat productivity (NDVI)	−2.55	3.84	−0.67	0.506
Mating season	0.58	1.27	0.45	0.651
Location factors				
Intensity of use of mapping unit	**3.85**	**1.13**	**3.40**	**<0.001**
Relative food availability in mapping unit	−0.02	0.02	−0.71	0.479
Relative group size	0.14	0.13	1.00	0.316

The final model was significantly different from the null model containing only individual nested within group and intergroup conflict as crossed random effects (likelihood ratio test: $N = 786$, $\chi^2 = 26.47$, $P < 0.001$, $R^2_{GLMM(c)} = 0.77$). Significant predictors are presented in bold.

DISCUSSION

The aim of this study was to determine how various costs and benefits influence female participation during intergroup conflicts in a wild population of vervet monkeys. Overall, we found that females were more likely to participate in intergroup conflicts that occurred in areas that were used at a high intensity over the long term, as well as in seasons when and in areas of their home range where high-quality food resources were most abundant at the time. These findings suggest that female vervet monkeys defend access to current food resources, as well as areas that their group consistently uses at a high intensity, regardless of present food availability. However, the important effect that rank had on the propensity for females to initiate and participate throughout intergroup conflicts, indicates that the benefits gained from defending these resources varied with position in the dominance hierarchy, and therefore priority of access to the defended

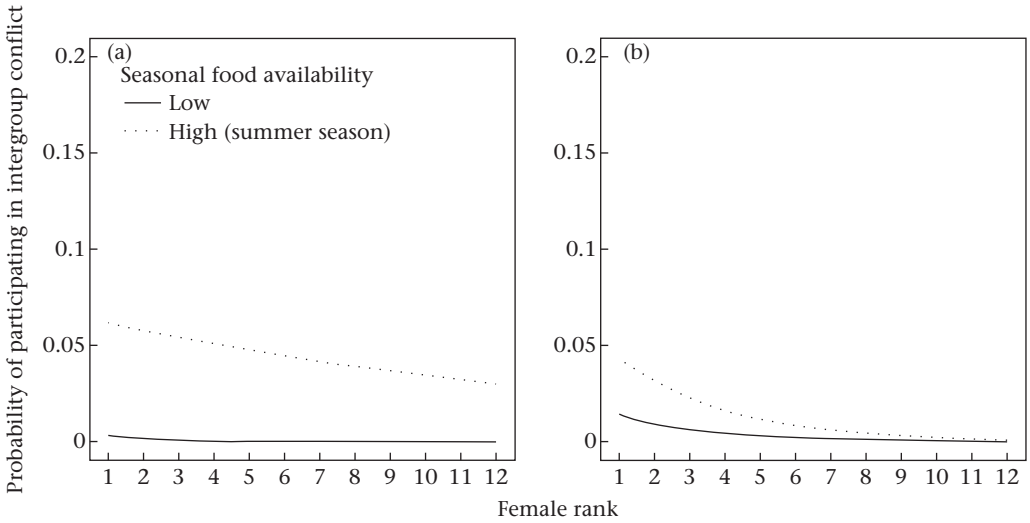

Figure 2. The probability that females participated aggressively during intergroup conflicts as a function of the three-way interaction between dominance rank (with '1' being the dominant female), seasonal resource availability and the relative availability of food within the contested mapping unit (compared to the rest of the home range). Prediction lines were obtained by plotting GLMM predictions (Table 2), setting all predictor variables not in the interaction term to their mean values when the variable was continuous or median values when the variable was binary. For visualization purposes, we set NDVI values to be above (dotted line) versus below average (solid line) to illustrate the effect that seasonal resource availability had on female participation. Similarly, we set the relative food availability to (a) a low value and (b) a high value to illustrate the effect that the spatial distribution of food had on female intergroup aggression.

Table 2
Factors affecting the probability that individual female vervet monkeys participated aggressively during intergroup conflicts

Fixed Effects	*B*	SE	*z*	*P*
(Intercept)	−9.40	6.35	–	–
Female characteristics				
Rank	−4.32	1.31	–	–
Had an infant	**−1.74**	**0.58**	**−3.03**	**0.002**
Seasonal factors				
Birth season	0.13	0.23	0.58	0.560
Seasonal habitat productivity (NDVI)	15.03	13.10	–	–
Mating season	2.57	1.59	1.62	0.105
Location factors				
Intensity of use of mapping unit	**3.30**	**1.41**	**2.35**	**0.019**
Relative food availability in mapping unit	9.68	9.47	–	–
Relative group size	0.24	0.16	1.49	0.137
Amount of male support during intergroup conflict	**3.34**	**1.62**	**2.06**	**0.039**
Interactions				
Rank * Seasonal habitat productivity * Relative food availability in mapping unit	**−8.22**	**3.11**	**-2.65**	**0.008**

The final model was significantly different from the null model containing only individual nested within group and intergroup encounter identity as crossed random effects (likelihood ratio test: $N = 786$, $\chi^2 = 70.65$, $P < 0.001$, $R^2_{GLMM(c)} = 0.93$). Significant predictors and interactions are presented in bold.

resources (Nunn & Deaner, 2004; Payne et al., 2003; van Schaik, 1989; Willems & van Schaik, 2015).

We found that females were less likely to participate in intergroup conflicts in years when they had infants, but more likely to participate when male group members were also participating aggressively throughout the intergroup conflict. These findings suggest that the perceived risk of injury, or costs of fighting, varied with female reproductive status and the behaviour of their larger male group members. Many studies have assumed that females with infants should be less likely to participate in high-risk intergroup conflicts (e.g. Crofoot & Gilby, 2012; van Schaik, 1996), but few studies have actually tested this assumption (Cords, 2007; Koch et al., 2016). We have demonstrated that female vervet monkeys decrease their level of activity during intergroup conflicts when they have an infant. As has also been reported previously (Cheney & Seyfarth, 1987), we observed infants being attacked by members of the opposing group. These attacks could result in death, indicating that intergroup conflicts can have very real fitness costs for females with infants, and may lead to risk-averse behaviour. Risk-averse behaviour was also evident among males who were likely to have sired offspring, as they tended to refrain from escalating intergroup aggression, and instead responded reactively when the opposing group was being aggressive (Arseneau et al., 2015).

Our finding that females were more likely to participate in intergroup conflicts when male group members provided high levels of support suggests that the perceived risk of injury associated with intergroup aggression is diminished when male group members also participate aggressively. Male vervet monkeys are approximately 1.5 times larger than females and have bigger canines, which probably makes them more valuable allies than group members of other age–sex classes. Females even use aggression as a punishment for nonparticipation, and this manipulative tactic effectively recruits male support in fighting for high-quality food resources (Arseneau-Robar et al., 2016). The value of consistent male support is further evidenced by the observation that when groups contained a male who was consistently highly aggressive during intergroup conflicts, members of opposing groups usually made no attempt to fight for the contested location (unless it was within one of their own intensely used mapping units), but simply fled. As a result, intergroup conflicts were brief, with a lower

opportunity cost than encounters in later periods (i.e. after this highly aggressive male emigrated), which could last for up to 8 h. Thus, males who consistently participate aggressively in intergroup conflicts may function much the same as 'impact hunters' (Gilby et al., 2015), reducing the perceived risk of injury for their female group members, and subsequently have a strong influence on the competitive ability of their group.

Classic sexual selection theory predicts that females should participate in intergroup conflicts primarily to defend access to food resources, and our findings support this in the case of vervet monkeys. However, we also found evidence that females defend valuable space. Females both initiated and were active throughout intergroup conflicts in mapping units that were consistently used intensely over the long term. These highly valued areas did produce abundant resources at some point each year, but were fought for regardless of present food availability. These intensely used mapping units probably contained other valuable resources, such as sleeping sites, but so did other mapping units that were not consistently defended. Alternatively, it is likely that as the philopatric sex, females know from experience which mapping units within their home range are the most productive and provide access to other important resources (e.g. sleeping sites and water). That females were more likely to initiate intergroup conflicts when in these intensely used areas suggests that they consistently tried to defend access to these areas, even if they were not always successful. Consistently defending these valuable areas may help establish ownership of them by negatively conditioning neighbouring groups at those locations. Although focal groups did not enjoy exclusive access to these valuable mapping units, neighbouring groups used these areas at a low intensity, suggesting avoidance. Thus, consistent intergroup aggression in intensely used areas may simultaneously limit scramble competition and avoid actual contests in the future.

In social species, competitive ability is typically thought to increase with group size (Mosser & Packer, 2009; Williams et al., 2004) but some studies have shown that smaller groups frequently win intergroup conflicts (Bonanni, Valsecchi, & Natoli, 2010; Crofoot et al., 2008; Kinnaird, 1992; Robinson, 1988; Sugiura et al., 2000; Zhao & Tan, 2010). When individual participation is highly variable, larger groups can suffer defeat if defection among group members is high (Crofoot & Gilby, 2012; Crofoot et al., 2008). Therefore, the decisions of individual group members, and subsequently the relative number of active participants, may determine the winner of intergroup conflicts (Zhao & Tan, 2010). Given that females usually outnumber males in vervet groups, females' decisions to participate versus defect should have a disproportionate effect on the relative fighting ability of a group. We observed considerable annual variability in birth rates, and groups therefore probably experience significant annual variability in their ability to win intergroup conflicts, being more competitive in years when few female group members give birth such that there are few risk-averse mothers. However, the potential for male intergroup aggression to elicit the participation of multiple female group members suggests that the decisions of individual males can have a disproportionate effect on the competitive ability of the group. The observed intra- and interindividual variability in the participation of males (Arseneau et al., 2015) indicates that temporal variability in group competitive ability is likely to be further exaggerated by changes in the composition and identity of male group members.

Although the amount of female support provided (i.e. intrasexual cooperation) probably also influences female intergroup aggression, we were unable to examine its importance in this study, as it was impossible to determine whether females were fighting together because they had a shared interest in defending resources or because they were cooperating with their female group members. Future work is needed to determine the extent to which intra- and interindividual variability in participation, as well as the effectiveness of both intra- and intersexual cooperation, impact group competitive ability. However, our findings, and those from previous work in this population (Arseneau et al., 2015; Willems et al., 2015), highlight that social groups are complex entities whose members each experience a unique set of costs and benefits in participating in cooperative intergroup aggression, and as a result, intra- and interindividual variability is often significant. Temporal changes in group composition, and the reproductive status of male and female group members, are likely to have very real consequences for the number of active participants, and thereby impact group competitive ability. This flexibility in competitive ability may help explain the absence of stable intergroup dominance relationships in a number of social species, and the persistence of relatively small groups (Crofoot et al., 2008; Perry, 1996; Robinson, 1988; Sugiura et al., 2000). Such findings improve our understanding of the extent to which intergroup competition exerts selective pressure on the evolution and maintenance of sociality (Bowles, 2009; Lehmann & Keller, 2006; West, Griffin, & Gardner, 2007; Wilson & Wilson, 2007; Wrangham, 1980; van Schaik, 1983).

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APPENDIX

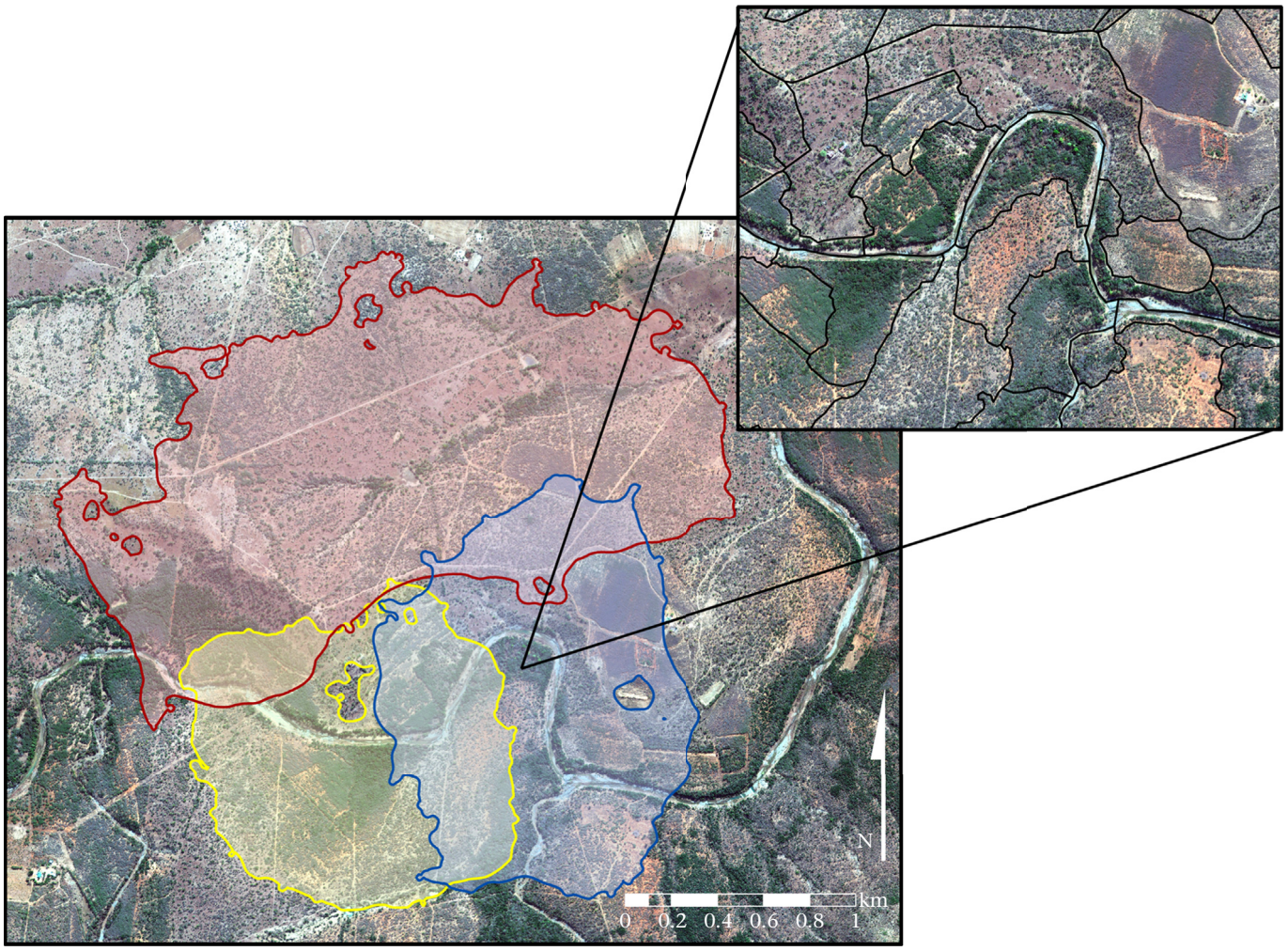

Figure A1. Map of the study area showing the three main study groups (yellow, red and blue polygons) and the mapping units (black lines) whose boundaries were delineated using abrupt changes in the vegetation density and composition, linear features (e.g. roads, fence-lines or the river), and the behaviour of the monkeys themselves.