Reactive and Pre-emptive Spatial Cohesion in a Social Primate

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Abstract

Spatial cohesion in group-living animals is assumed as a risk-sensitive characteristic. Few studies have explicitly investigated this assumption or asked whether risk-related changes in spatial cohesion operate over short or long-term scales. We explored whether two groups of wild samango monkeys (*Cercopithecus albogularis schwarzi*) adjusted cohesion in reaction to naturally occurring risk from eagles and inter-group encounters using the number of conspecific neighbours as our response. Data on these directly observed encounters were used to assess reactive responses to immediate events. GPS-recorded locations of these encounters allowed us to create relative risk landscapes to investigate whether these groups might pre-emptively increase cohesion in high risk locations, in the absence of a direct threat. Multi-model inference was used to compare support for candidate models representing biological hypotheses. We found support for changes in cohesion in reaction to immediate inter-group conflict in both study groups. In contrast, only eagle risk apparently elicited a pre-emptive response. These results suggest that spatial cohesion is risk-sensitive, but that responses differ between types of risk and between groups.

Introduction

Spatial cohesion in animal social groups refers to the extent to which members maintain inter-individual proximity. This type of cohesion is important for the stability of groups (Trillmich, Fichtel, & Kappeler, 2004). Individuals benefit from cohesion through greater protection from predators, due to safety in numbers (Bertram, 1978; Elgar, 1989; Zhao et al. 2019), and enhanced access to social information about potential risks or resources (Evans et al. 2016; Fernández-Juricic, & Kacelnik, 2004). While animals can reactively adjust their behaviour to the immediate environment, they can also make decisions based on information gathered from previous experience and memory (Bracis & Mueller, 2017; Broekhuis et al. 2013; Dröge et al. 2019). This prior information might also lead animal groups to pre-emptively alter their spacing where they perceive greater risk. In this study we address the question of whether a wild social primate – the samango monkey (*Cercopithecus albogularis schwarzi*) – might flexibly adjust spatial cohesion in response to both immediate risks (reactive increase) and pre-emptively in response to variation in risk perception across the landscape.

Predation and spatial cohesion

Social prey species often perceive themselves to be under greater risk when they have fewer conspecific neighbours nearby (e.g. Fernández-Juricic et al. 2007), and numbers of immediate neighbours may be a more important determinant of individual risk perception than absolute group size (Treves, 1998). There is also evidence that cohesion itself is sensitive to variation in perceived risk. Chivers et al. (1995) used experiments with predator chemical cues on groups of fathead minnows (*Pimephales promelas*) and found that the groups became tightly cohesive post-exposure. Similarly, observations of hamandryas baboons (*Papio hamadryas*) indicated that groups maintained closer spatial cohesion on mornings after a group had encountered a night predator (Schreier & Swedell 2012). Domestic sheep (*Ovis aries*) have also been found to reactively aggregate when targeted by trained dogs (King et al. 2012).

Behavioural responses to risk can operate over both short-term scales in response to immediate danger and over long-term scales, such as with landscape-level variation in predation risk (Dröge et al. 2019). Even in the absence of a direct threat, experience with risky habitat types or locations might elicit pre-emptive responses

based on prior knowledge (Fagan, 2013). The ability to perceive these differences in safety allows prey species to shift their behavioural strategies or space use accordingly (Arias-Del Razo et al. 2012; Laundré, Hernández, & Altendorf, 2001; Willems & Hill, 2009). Pre-emptive responses can reduce the probability that individuals or groups will encounter a predator and be forced to react to an immediate threat. For example, smaller groups of wild bison (*Bison bison*) selected safer habitats compared to when the same individuals formed larger groups (Fortin et al. 2009). Yet, whether social animals alter within-group spatial cohesion in response to locations where they have had prior encounters with predators or other dangers is uncertain.

Previous research at our study site indicates that risk from eagles is an important determinant of samango landscape utilization (Coleman & Hill, 2014). Moreover, observers recorded predatory encounters between these species relatively frequently (personal observation). Research on this study population also indicates that humans modulate samango risk perception from terrestrial carnivores (Nowak et al. 2014). Thus, this study is focused on the more commonly encountered eagle predators.

Inter-group competition

Collective inter-group defence has been observed across a variety of group-living species including social carnivores, birds, and primates (Heinsohn & Packer, 1995; Müller & Manser, 2007; Radford et al. 2016). Such conflict can be risky (Radford et al. 2016; Shopland, 1982), and evidence suggests that maintaining spatial cohesion with other group members may be important for effective defence and individual safety. For example, male West African chimpanzees (*Pan troglodytes verus*) in the Tai Forest remain relatively cohesive even while foraging in separate parties, presumably because inter-group conflicts may require collective action (Eckhardt et al. 2015). Upon detecting the scents of other groups, banded mongoose (*Mungos mungo*) emit calls that result in recruitment of fellow group members and direct encounters often include collective aggression (Müller & Manser, 2007). Following aggressive inter-group encounters, cohesion may also be high when many individuals engage in affiliative behaviours as a result of stress/anxiety (Radford et al. 2016) or ongoing perceptions of conflict risk. If an animal or group behaves pre-emptively towards landscape/habitat level variation in perceived predation risk, then it may follow that perceived risk of inter-group competition may also result in similar

responses. Previous studies that have focused on competition between sympatric carnivore species have found evidence that smaller species avoid locations where they might encounter larger competitors (Berger & Gese, 2007; Broekhuis et al. 2013). However, we found fewer examples of prey species exhibiting similar shifts with regards to intraspecies conflict (but see Benadi, Fichtel, & Kappeler, 2008). Yet, if groups need to maintain cohesion to collectively defend against competitors, then we might expect individuals to pre-emptively seek proximity to their group members in areas of heightened risk. Doing so could provide greater safety, enhance individuals' abilities to engage in conflict, and/or facilitate information transfer for early warning about potential threats.

Samango inter-group encounters typically involve aggression from only adult females (Lawes & Henzi, 1995; Henzi, Payne, & Lawes, 2003). One report described female group members attacking and killing a dispersing female (Payne, Lawes, & Henzi, 2003), but other studies report that few conflicts result in physical aggression (Henzi, et al. 2003). Prior research on our samango monkey population found that study groups tended to avoid areas of high eagle risk, but not areas of high inter-group encounter risk (Coleman & Hill, 2014). One possible explanation for this is that prey species that are already constrained by the need to avoid predation might employ other pre-emptive strategies to mitigate this additional risk. Additionally, groups may not preferentially avoid areas where inter-group conflict is high because they may be resource rich (Brown, 2013), and engaging in competition may maintain ranging area and outweigh the potential costs.

Additional social and ecological variables

In this study we focus on whether spatial cohesion in a social primate might be risk sensitive and whether these responses are reactive and/or pre-emptive. To investigate these questions, additional variables need to be accounted for that could also plausibly influence spatial cohesion. Among these are variation in the number of group members engaged in social behaviours which necessarily require proximity, variation in the immediate availability of food sources, and local habitat characteristics. For example, greater amounts of within-group competition should result in disaggregation (Heesen et al. 2015). Conversely, higher rates of

affiliative social behaviours should result in short-term increases in cohesion (Sugiura, Shimooka, & Tsuji, 2011).

The effect of the immediate availability of high-quality, spatially clustered food items on spatial cohesion might also be mediated by a species' tendency towards high or low levels of intra-group feeding competition. Heesen et al. (2015) observed that wild Assamese macaques (*Macaca assamensis*) were less cohesive while feeding, while hamandryas baboon bands were more likely to break into one-male units when foraging in habitats with lower food availability (Schreier & Swedell 2012). Both observations were potentially due to animals foraging away from group members to avoid contest competition. Other species may aggregate more closely while foraging, because individuals might take advantage of social information to locate food items (Dall et al. 2005), or because a patchy distribution of food across the environment facilitates clustering within a small area. Red-tailed monkeys (*Cercopithecus ascanius*) (Bryer et al. 2013), patas monkeys (*Erythrocebus patas*) and vervets (*Chlorocebus pygerythrus*) (Isbell & Enstam, 2002) all tend to forage more closely to conspecifics when feeding on fruits which are rarer and more spatially clumped than leaves or insects. Here we account for variation in social and foraging behaviour by the inclusion of control variables in all our models to better estimate the effects of risk.

Characteristics of individual groups, including group size and demographics may be important predictors of typical levels of cohesion. While beyond the scope of this study, it is important to note that as group size increases, feeding competition may also increase in many primate species (Janson, 1988; Janson & Goldsmith, 1995), leading to differently sized groups varying in cohesion. Additionally, larger groups may be more likely to attack a competing group and 'push' competitors away (Furrer et al. 2011; Wilson et al. 2012), although this is not always the case (Crofoot et al. 2008). Thus, different groups will likely differ in how they respond to environmental variation. Here we use data on two relatively large groups and therefore cannot investigate this, but we account for potential effects of group identity throughout our analysis.

Habitat characteristics such as visibility should limit the ability of individuals to monitor others (Fernández-Juricic et al. 2007). Low visibility may lead individuals to seek proximity to group mates, increasing their overall cohesion, or, conversely, losing track of neighbours and becoming disaggregated.

Visibility is also often related to the likelihood of detecting an approaching or hiding predator (Fortin et al. 2009). Previous research on our population of samangos indicated that this population avoids areas of low understory visibility, independently of variation in the spatial distribution of resources (Coleman & Hill, 2014). Canopy cover may, however, impact perception differently in this species, because areas where vertical visibility is high could be riskier for monkeys because they may be more easily targeted by aerial predators (Shultz, 2001), although some cover should be necessary for an eagle to ambush monkeys from within the canopy (Shultz, Noë, McGraw, & Dunbar, 2004).

Present study

We used handheld Global Positioning Systems (GPS) data and direct behavioural observation of samango monkeys collected over 17 months in the Afromontane forests of northern South Africa to examine potential associations between spatial cohesion and risk at two different temporal scales. Our response and proxy for spatial cohesion was the number of conspecific neighbours counted within scan samples. Specifically, we hypothesized that:

1. Samangos would exhibit reactionary changes in cohesion to immediate risk. We predicted that groups would become more cohesive while threatened by competitors or predators.

2. Samangos would pre-emptively alter spatial cohesion in response to location-specific risk in the absence of any direct threat. Thus, we predicted that cohesion might change along with variation in location-specific risk, rendering reactionary responses to threats unnecessary.

To investigate these hypotheses, we compared sets of plausible candidate models (Table 1) (Burnham, Anderson, & Huyvaert, 2011) while controlling for variation in the immediate availability of relatively rare food sources, habitat characteristics, group identity, and potential variation in within-group social behaviour and. We then use top models to further investigate these predictions.

Methods

Study Site & Species

We conducted our study at the Lajuma Research Centre in the western Soutpansberg Mountains of Limpopo, South Africa (23˚02'S, 29˚26'E) using long-term data collected by the Primate and Predator Project. The study site encompasses an array of habitat types including tall moist Afromontane forest, deciduous woodland, acacia bush, and rocky grassland/cliffsides. We studied two samango groups, "Barn" (N~35) and "House" (N~70-80), that were well-habituated to direct observation. Samangos are medium sized (adult females ~ 4.4kg, adult males ~ 7.6kg), arboreal, mainly frugivorous monkeys that live in single-male multi-female groups typically with 10 to 65 individuals (Coleman & Hill, 2014). Natural predators of samangos at this site include crowned eagles (*Stephanoaetus coronatus*) and black eagles (*Aquila verreauxii*), the African leopard (*Panthera pardis*) (Chase Grey et al. 2017), caracal (*Caracal caracal*) (Nowak et al. 2014), and, potentially, rock pythons (*Python sebae*). While samangos at this site face risk from multiple predators, we focus on predation from raptors in this study because previous research has shown them to be the primary driver of space use in this environment (Coleman & Hill 2014). We do not distinguish between eagle species in our analysis.

Ethical note

We received research permission from the Limpopo Province Dept of Economic Development and Tourism (Permit # ZA/LP/81996). This research was also approved by the University at Buffalo IACUC (#ANT07037N) and Durham University Animal Welfare Ethical Review Board. All project members and research assistants collecting direct behavioural data on these habituated groups received training and protocols to maintain human/animal safety through the Primate and Predator Project. Observers were trained to observe animals with binoculars from a distance, avoid direct eye contact, and any other potentially disturbing behaviours to minimize observer bias and potential stress to animals.

Behavioural Data Collection

Behavioural and location data were collected from August 2016 until December 2017. We collected data on each study group from dawn to dusk, three to four days a week via scan sampling (Altmann, 1974); the behaviour of as many individuals as possible within the group was recorded during a five-minute window every 20 minutes throughout the day. Study days ranged from a minimum of 10.5 hours (0640 – 1720) in the austral winter to a maximum of 14.5 hours in the summer (0440 – 1900). Most individuals within both groups were not individually recognizable. We minimized the possibility of repeating samples on the same individual within a 5-minute scan by moving throughout the group and collecting data only when we were certain we had not previously recorded an individual. Within scans we recorded the time, date, group ("House" or "Barn"), individual age-sex class, and identification when an individual was known. We used five general behavioural categories of "feeding", "resting", "socializing", "moving" or "other" and recorded more specific categories within each of these. When an individual was feeding, we attempted to identify the plant or insect species and recorded the type of food item taken. When two or more individuals were grooming one another we only sampled one individual (the first one an observer saw). Additionally, we recorded the number of non-infant neighbours each individual samango had within 5 meters as a proxy for group cohesion. This included neighbours within 5 meters that were above or below the sampled individual. This method follows Treves (1998, 1999b) on the closely related blue monkey (*C. mitis*). As the number of individuals sampled varied between 5-minute scan windows, we accounted for this in our analysis (see statistical analysis). The distance of 5-meters was chosen as a balance between collecting neighbour data and remaining accurate through low-visibility habitats. We minimised bias and attempted to obtain data representative of the whole group by moving positions with each subsampled individual from the centre to the periphery and sampling between subgroups. This should have given us a relatively realistic picture of overall group spatial cohesion during a 5-minute sample, regardless of absolute group size.

Along with each scan sample, we collected a GPS point with a handheld device (Garmin GPSmap 60Cx or 62s, Garmin, Olathe, Kansas, US) prior to behavioural data collection. We recorded the location and details of all predator encounters, inter-group encounters, alarm vocalizations, and within-group aggression *ad libitum.*

In this dataset we included eagle predation attempts and encounters that elicited alarm vocalizations from group members but did not include in our analysis observations of large birds flying overhead if subjects did not react. Responses to inter-group conflict ranged from alarm vocalizations to direct aggression and chasing. For most of these encounters there was no obvious "winner" of the conflict. We later noted whether an encounter had occurred during or within 5 minutes of the beginning of a scan sample window. Encounters occurring outside this time may have less of an effect on behaviour and therefore we excluded these data (and subsequent 20, 40, and 60-minute scans).

Nineteen observers (including X.X. and X.X.) collected behavioural data. Training in data collection, including identification of food plant species, lasted approximately one month (between 3 to 5 weeks). Assistants were trained by X.X. to navigate between the periphery and centre of (sub)groups confidently within and between scan samples. This was to ensure as much of the group was sampled as possible consistently throughout the day. Regular testing and monitoring by X. X. ensured assistants did not follow single smaller subgroups for the duration of observation days and scan windows. At the end of this period each trainee was observed by X.X. over the course of a full follow day or until several hours of consecutive instantaneous scans were in complete agreement with those of X.X. to ensure inter-observer reliability. Trainees collected data independently only after successfully completing this assessment and were then subject to checks by X.X. to ensure consistency.

Vegetation and Habitat Data

We collected vegetation data in $25m^2$ quadrant randomly distributed across the home ranges of the two samango groups to measure habitat visibility, canopy cover, and to collect information on the size and distribution of fruiting tree species following Brower, Zar, and Von Ende (1998), Coleman and Hill (2014), and Willems and Hill (2009). Coleman and Hill (2014) found visibility measured in similarly designed 5m x 5m plots was a significant predictor of landscape use in this samango population, indicating that these methods measure variables on a scale relevant for this species. In each plot, we measured horizontal habitat visibility in each cardinal direction at five meters and 10 meters from each plot corner using photographs of a one-meter by

one-meter checkerboard with 225 squares. The percentage of the board that was visible was averaged across these photographs for one measure of horizontal visibility. Canopy cover was measured through photographs taken directly upward through a one-meter by one-meter square held parallel to the ground. We then used ImageJ (Rueden et al. 2017; National Institutes of Health, Bethesda, Maryland, USA) to calculate the number of dark pixels to estimate the percentage of the photo that was foliage as a proxy for canopy cover. To obtain location-specific values for horizontal visibility and canopy cover, we created rasters using location and attribute data from 905 vegetation plots distributed randomly across the home range of each group using the open-source software RStudio 3.5.0 (R Core Team 2018) and the packages "raster" (Hijmans et al. 2017) and "sp" (Pebesma et al. 2018) with a resolution of 25 meters. For those cells that contained more than one point, we obtained the mean of the attribute values. We used location data collected alongside behavioural scan samples to extract attribute data based on the nearest grid cell (supplementary figures 1 – 6). Thus, for every scan sample location we obtained a value for canopy cover and understory visibility.

We also collected data on all trees within each vegetation plot that we identified as mature individuals (>10 cm circumference at breast height) and listed the species when possible. Any trees that were located on the boundary rope of the plot were sampled if any part of the main stem/trunk was within the plot. Previous studies (e.g. Coleman & Hill, 2014b) and scan-sampled data allowed us to identify food plant species important for samango monkeys at this site. Of these food species, we further identified which produced fruits and had large crown diameters that could potentially support a large proportion of a foraging samango group (mean crown of ≥10 meters). From this information we then ranked these trees by relative abundance and identified the 10 rarest species that could support co-feeding as *Ficus burkei, Ficus craterostoma, Ficus sur, Ekebergia capensis, Acacia sieberiana, Trychillia dregeana, Rauvolfia caffra, Syzygium cordatum, Croton sylvaticus,* and *Celtis africana.* Behavioural scan data on the number of individuals feeding on these species was then used to calculate the proportion of a sample feeding on these relatively rare and large fruiting trees and this variable was included as a control in all models.

Relative Risk Data

We created maps for the relative risk of inter-group encounters and eagle encounters for every month of the study period to assess whether groups might pre-emptively increase cohesion in risky areas. We created kernel density estimates (KDEs) of each type of risk per each group based on GPS recorded locations of eagle encounters and inter-group encounters. The values for risk for each observation were based on the previous 12 months of data collection, with these data from August 2015. Therefore, events that happened later than an observation, but during the same month, were not included. We created these density estimates with the R package adehabitat (Calenge, 2006) and used plug-in bandwidth selection which performs well for small sample sizes (Gitzen, Millspaugh, & Kernohan, 2006). We created kernel density estimated utilization distributions (UDs) using GPS data collected during scan samples. These were similarly created from the previous 12 months for each month of observations. In total, we created 17 KDEs of eagle encounters and 17 KDEs of inter-group encounters for each group to be paired with the same number of UDs. We then converted density estimates to rasters and divided each month's eagle encounter and inter-group encounter density estimate by its UD to obtain monthly risk values for both types of threat relative to how frequently locations were used (Figure 1). This method corrects for how often we observed samangos in a particular location to ensure areas visited more frequently were not erroneously weighed as being riskier than more rarely visited areas. We used these location-specific risk values as predictors for perceived eagle risk and perceived inter-group encounter risk to assess whether groups might pre-emptively change their cohesion in the absence of a direct threat following Willems and Hill 2009 and Coleman & Hill 2014. Importantly, these relative risk maps represent where samangos might be more likely to perceive themselves as being at risk of encountering an eagle or competing group due to previous experience while under observation. We do not assume this method creates a landscape of intrinsic risk that is consistently true for when groups are unobserved by a human. As previous studies on this species have found that perception of risk of terrestrial predators is modulated by a "human-shield," their overall landscape of risk is likely somewhat different when not in the presence of researchers (see discussion).

Statistical Analysis

Our analysis focused on behavioural samples collected in the hour preceding and following 144 inter-group encounters and 74 eagle encounters and predation attempts. Our response variable was the total count of nearest neighbours across all individuals included within a 5-minute scan window. We offset the response by the number of individuals that we collected data on during a sample in all our models to account for this variation. When an offset is added to the equation, the rate is modelled, allowing the response to vary with the exposure (number of samangos sampled in a scan window) (Brooks et al. 2017). We restricted scan samples to those in which data were collected on 5 or more individuals for a total of 1129 scan samples clustered within 218 events.

Our predictor for reactionary changes in cohesion to immediate risks was a categorical variable that denoted whether a behavioural sample occurred in the absence of either of these events (baseline), during (within 5 minutes) of an inter-group encounter (IGE) or eagle encounter (EE), or whether the sample was collected 20, 40, or 60 minutes following these events. The duration of eagle encounters tended to be short and only occur within one behavioural sample while conflicts between groups often lasted through two or more samples. If an inter-group or eagle encounter occurred outside of a scan sample window (or within 5 minutes of a sample) then we excluded that data. Scan sample locations (UTM) were used to extract eagle and inter-group encounter relative risk values for each line of data.

We compared several candidate models for group spatial cohesion using an information-theoretic framework to conduct multi-model inference. We preferred this approach to null-hypothesis testing because Akaike weights provide a quantitative measure of empirical support for each alternative model, given the observed data. This procedure is also appropriate given that our hypotheses are non-mutually exclusive and works for both nested and non-nested models (Burnham et al. 2011). We used the small sample corrected Akaike Information Criteria (AICc) as this criterion works well for a range of sample sizes. Our null model assumed that risk variables were not good predictors of cohesion but included habitat and behavioural variables likely to be important. Our other models included at least one pre-emptive or reactionary risk variable so we

could compare support between these and to the null. For a list of predictors included in each candidate model see Table 1

Our response variable was over-dispersed, therefore we fit the data to Poisson mixed effects models with a random effect for each scan sample using a unique ID to account for this moderate amount of variance past the mean (Harrison, 2014) using the R package GLMM Template Model Builder (glmmTMB) (Brooks et al. 2017). In all models, the random effects of the time of the scan sample were crossed with a unique ID for each event (one of the 218 clusters). We further checked assumptions and simulated residuals for spatial and temporal autocorrelation in a maximal model using the package DHARMa (Hartig, 2017). While we did not detect significant spatial autocorrelation, we included a spatial random effect within all models to account for non-independence between points located closely together (based on Euclidean distance, Brooks et al. 2017). Because we used models with a log link, our response offset is included as the natural log of the number of individuals we sampled within a scan. All models included the fixed effects of "group" to account for potential variation due to group identity. We further included the number of within-group aggressions that occurred up to the time of each scan sample and the proportion of individuals engaged in affiliative social behaviour (play, grooming) at the time of a sample in all models as control variables.

Habitat visibility measures (understory, canopy) and the proportion of sampled individuals feeding on rare fruiting trees were also included in all models to account for these potential effects. However, because habitat attributes might affect predation risk in this species (Coleman & Hill, 2014), we included this variable as an interaction term in certain models because location-specific risk perception may depend on habitat structure as well as previous experience. Finally, our predictor for feeding/foraging behaviour was the proportion of individuals within a behavioural scan sample feeding on fruits of the large and rare species identified from vegetation plots. This predictor was chosen rather than quantifying the absolute amount of food in a given patch because short-term changes in group-level feeding behaviour could affect overall cohesion (e.g. Bryer et al. 2013; Isbell, & Enstam, 2002). Our reasoning for this choice was that resource availability may not necessarily influence cohesion when individuals are engaged in non-feeding activities.

We considered the "best" models to have the highest model weights and lower ΔAICc (Δ_i) values (Anderson & Burnham, 2004; Richards et al. 2011) and present parameter estimates of these top models. Commonly used practice considers Δ_i <2 to be practically equivalent and models with Δ_i <6 not discounted (Anderson & Burnham, 2004; Richards, 2005). Many do not recommend to model averaging coefficients of discrete distributions or models with random structures (Cade, 2015). However, estimates of fixed effects we present here show only small differences and no change in sign/direction, which also renders model averaging predictions unnecessary (Bolker et al. 2009). We do not present *p*-values for these coefficients for assessing parameter importance as much evidence indicates these values may not be reliable for inference in final models (Brewer, Butler, & Cooksley, 2016; Freedman & Freedman, 1983). Furthermore, these values do not necessarily translate to biological significance (Burnham et al. 2011). We assess trends with variables of interest using model predictions (and their 95% prediction intervals) and marginal effects while holding other variables at their mean or reference values for improved inference (model summaries including p-values, supplementary table 3). This allowed us to investigate our reactionary versus pre-emptive questions separately by removing reactionary effects to look at potential pre-emptive changes between high and low risk locations in the absence of a direct encounter. We calculated and plotted values transformed back to counts of nearest neighbours using the ggeffects package to visualize the influence of each variable on the response (Lüdecke, 2018). Random effect variance was set to zero for calculating population-level values. Additionally, we used the package sjstats (Lüdecke, 2018) to calculate inter-class correlation coefficients (ICC) for the random structure of our models. Finally, we calculated the marginal and conditional pseudo-R^2 of each model following Nakagawa and Schielzeth (2013) to provide information about the explanatory ability of each model.

Results

Our dataset included 1129 scan samples clustered into 218 events (144 inter-group encounters and 74 eagle encounters). Two of our candidate models fit our criteria as potentially being the 'best' fitting model of the set. These were model 1 representing reactionary changes to eagle or intergroup encounters and model 3 combining reactionary changes and pre-emptive changes with no interactions (Table 2). This initial selection

provides evidence that both reactionary and pre-emptive responses to risk may occur. Estimates for parameters found in both models were similar in magnitude and direction (supplementary table 3). Our control variables for within-group behaviour (aggression and affiliative social behaviour) both appeared to be predictors of increased cohesion (supplementary figures 1 and 2) and were thus important to account for. Additionally, we noted a small positive association between feeding on relatively rare fruiting trees and cohesion (supplementary figure 3) but estimates for this variable were close to zero and its prediction intervals were wide. Finally, neither understory visibility nor canopy cover appeared to be strongly associated with our measure of group spatial cohesion.

ICC values for random effects indicated that time of day the scan sample occurred did not explain any variance (0.0) in the response while the proportion explained by 'event ID' was 0.254 and the proportion explained by geographic location was 0.213. These indicate that cohesion is relatively consistent within the same day and between instances when groups returned to the location of a raster cell. Marginal pseudo-R^2 values which approximate the variance explained by the fixed effects indicate that our candidate models explained between 12.86 to 15.03% of the variation in cohesion. Conditional values indicate that combined fixed and random effects explained between 52.73 to 55.12% of the variation in cohesion (Table 2).

Hypothesis 1: Samangos would exhibit reactionary changes in cohesion to immediate risk

During baseline observations, Barn group tended to be more cohesive with ~10 neighbours per scan sample versus House with ~7 (Figure 2) (total number of individuals scanned held constant). Estimates from both top models indicated that our variable for reactionary responses to risky events was mainly informative due to the inclusion of inter-group encounters and the immediate aftermath (20 minutes) of those events. Coefficients in these two models were the same (β+SE=0.364 ± 0.076) and their 95% confidence intervals differed only slightly (model 1: 0.215, 0.514; model 3: 0.211, 0.509).

We used model 3 to estimate the predicted change in the number of neighbours per scan sample during encounters to account for location-specific risk. During inter-group encounters Barn group would gain ~4 – 5 individuals per sample ($\hat{y}$=4.865, 95% PI: 3.852, 6.077) while House group would gain ~3 individuals

($\hat{y}$=3.249, 95% PI: 2.543, 4.107). Counts of neighbours were somewhat elevated 20 minutes following these

events (Barn: $\hat{y}$=1.328, 95% PI: 0.632, 2.206; House $\hat{y}$=0.887, 95% PI: 0.427, 1.479) but samples at 40 and 60

minutes overlapped baseline values.

Eagle encounters did not apparently elicit any change in cohesion over baseline values (model 1:

β+SE=0.02426 ±0.099; model 3: β+SE=0.020 ±0.098) and there was no apparent change in the 20, 40 or 60

minutes after these events (Figure 2).

Hypothesis 2: Samangos would pre-emptively alter spatial cohesion in response to location-specific risk in the

absence of any direct threat

In the absence of any direct threat (holding the 'event' variable at baseline/reference values) relative

inter-group encounter risk was not strongly associated with number of neighbours/spatial cohesion and values in

high risk locations overlapped with low risk (β+SE=0.209 ±0.287, 95% CI: -0.354, 0.763) (Figure 3).

In contrast, we found an apparently positive association with increasing eagle risk. The coefficient for

this term in model 3 overlapped zero (β+SE=0.89 ±0.51, 95% PI: -0.11, 1.89) which may reflect differences

between the two samango groups in their response. In areas of the highest risk (upper quartile), Barn group

tended to have ~5-6 more nearest neighbours within a scan sample than when in areas with the lowest risk

($\hat{y}$=5.788, 95% PI: 2.946, 9.678). House tended to have ~4 more individuals ($\hat{y}$=4.105, 95% PI: 0.760, 6.848)

(Figure 4), but its lower prediction interval was close to zero (as compared to baseline).

We originally predicted that if an encounter event occurred in a high-risk location, pre-emptive

responses could remove the need for reactionary ones. To investigate this, we calculated predicted values for

encounters only in areas of lowest risk. Reactions by Barn group to inter-group encounters in low risk areas

resulted in an increase by ~4 neighbours per sample ($\hat{y}$=4.734, 95% PI: 3.554, 6.349) and this was roughly the

same as in high risk locations ($\hat{y}$=4.852, 95% PI: 3.662, 6.321). Reactions by House resulted in an increase of

~3 individuals in both low ($\hat{y}$=3.162, 95% PI: 2.081, 4.223) and high-risk locations ($\hat{y}$=3.241, 95% PI: 2.416,

4.273). Similarly, we found no change to samango responses to eagle encounters while in low risk locations (1st

quartile) (Barn group: $\hat{y}=0.017$, 95% PI: -0.71, 1.053; House group: $\hat{y}=0.012$, 95% PI: -0.426, 0.629). As only a few points existed with relative risk of zero, we could not examine changes at the minimum value.

Discussion

We investigated whether samango monkeys flexibly adjusted their group spatial cohesion in response to immediate changes in ecology and whether groups responded pre-emptively based on previous experience at a particular location. In the absence of any immediate events (inter-group or predator encounters), and when both location-specific risk and the proportion feeding were held constant at their means, our two groups tended towards different levels of cohesion. Specifically, individuals within our House group tended to have fewer neighbours than individuals within our Barn group. Yet, both similarly displayed reactive responses to inter-group conflict and no apparent response to eagle encounters. Neither group strongly increased cohesion in areas of high inter-group encounter risk, but we found a slight positive trend, potentially indicating why this variable appeared in our top model set. In contrast, Barn group may pre-emptively increase cohesion in areas of high eagle risk, but we found less evidence that House group responded similarly. Finally, reactionary responses to both inter-group encounters and were similar regardless of the level of location-specific risk.

Hypothesis 1

Inter-group encounters often resulted in individuals collectively making threats and chasing members of the competing group. For an individual, attacking a competing group may be less risky while in greater proximity to other group mates (Eckhardt et al. 2015). Additionally, because many individuals target competitors simultaneously, spatial cohesion is likely to be high during these events. This result contrasts with our findings for immediate risk for eagle encounters where we did not detect substantial changes in cohesion for either group. This was unexpected given that previous studies have found that risk from aerial predators may be a stronger predictor than inter-group conflict or resource availability for space use in samangos at this site (Coleman & Hill, 2014). Under immediate predation risk, we expected that subjects would seek proximity to conspecifics or that many individuals would seek cover in similar locations, resulting in increased cohesion.

This finding that cohesion did not immediately increase is also in line with previous findings for blue monkeys; Treves (1998) found that elevated risk perception was associated with greater numbers of nearest neighbours, but also that individuals did not increase their spatial cohesion following playbacks of predator sounds (Treves, 1999). Similarly, in a study of grey-cheeked mangabey (*Lophocebus albigena*) reactions to crowned eagles, Arlet and Isbell (2009) found that the most commonly observed reaction to eagle predation attempts was sitting still. While Schreier and Swedell (2012) found that hamandryas baboons were more cohesive in the mornings following predator encounters, their observations were recorded in the hours following a threat, suggesting that longer-term perceptions of risk, rather than the immediate reaction to a predator encounter, resulted in increased cohesion. Thus, while increased numbers of nearest neighbours may provide enhanced access to social information that could mitigate risk (Fernández-Juricic & Kacelnik, 2004), reactively increasing cohesion may not be an effective strategy for this primate species to avoid mortality from aerial predators.

Hypothesis 2

Variables for both forms of location-specific relative risk measured here were included in the top model set. Increasing eagle risk was associated with an increase in cohesion for the Barn group but this was only weakly true for the House group. In comparison, we did not find strong support for an association between inter-group encounter risk and cohesion. However, we cannot rule out that a weak effect may be more pronounced in a study including more than two interacting habituated groups or a greater sample size. Thus, we found some mixed evidence for cohesion being sensitive to long-term variation in risk. This difference between risk from predation versus competitors may reflect the fact that conflict between groups does not always result in direct physical aggression. Additionally, if groups are able to hear an oncoming group from a distance and reactions lead to greater cohesion, then pre-emptive responses may not always be necessary. In contrast, if reactive changes in cohesion do not help individuals evade aerial predators, pre-emptive responses may still reflect landscape-level variation in risk perception and could help individuals learn about the presence of predators more quickly. Once an aerial predator or alarm is detected, individuals might choose to remain still if moving makes them more conspicuous.

We used our model including both relative risk and event variables to assess whether pre-emptive increases in cohesion in high risk locations would render reactionary responses unnecessary but found no evidence to support this prediction. Future studies using methods other than direct observation might investigate this with risk from terrestrial carnivores as our sample size allowed us to focus on risk only from eagles (LaBarge et al. 2020). Strategies for evading other predators could also include a greater reactionary change in cohesion.

These results, combined with previous studies on samangos avoiding areas of high perceived predation risk (Coleman & Hill, 2014), may indicate that this species can remember where they have previously encountered danger. Evidence from other species, including other primates, suggests that this is plausible (Cunningham & Janson, 2007; Fagan et al. 2013; Garber, 1989). Thus, further investigation into the role of spatial memory in predation or conflict avoidance may be a promising area of future research.

Additional ecological variables

Habitat attributes, including horizontal visibility and canopy cover are often associated with predation risk (Fortin et al. 2009) and the ability of individual animals to monitor one another (Fernández-Juricic & Kacelnik, 2004; Frechette, Sieving, & Boinski, 2014) but our models that included interactions between location-specific risk or risky events and habitat attributes (models 2, 7-8) had relatively low weights. This was unexpected because previous studies of predation on forest primates indicated that crowned eagles often attacked where canopy cover was relatively low (Shultz, 2001) and previous studies on this population indicated that understory visibility was a significant predictor of perceived risk (Coleman & Hill, 2014; Emerson et al. 2011). A possible explanation for this is that subcanopy structure and the presence of sturdy branches to perch and ambush monkeys are also important for how successful an eagle might be in an attack. Additionally, while we used similar visibility sampling methods as Coleman and Hill (2014), understory visibility may be more important for risk from terrestrial predators. We did not attempt to sample risk from these predators because encounters were too infrequent and our presence during observations may have modulated risk from these species because many terrestrial carnivores are intolerant of proximity to people (Ngoprasert, Lynam, & Gale,

2007; Smith et al. 2017). Furthermore, previous studies on this population indicate that humans might reduce samango risk perception of these terrestrial carnivores while observed (Nowak et al. 2014). This could mean that risk landscapes or within-group spatial patterns are significantly different for these groups while not in proximity to humans. Risk landscapes for inter-group encounters may also differ because unhabituated primates often avoid contact with humans (Williamson & Feistner, 2003). Thus, future research should attempt to measure cohesion through means other than direct observation such as using high fix-rate GPS collar data or coupling GPS collar locations with data from proximity sensors (Handcock et al. 2009).

We included the proportion of the group feeding on important fruiting trees as a control variable in all our models. While this variable was not apparently significant, we did find a small positive trend in our marginal effects where cohesion increased along with this variable. While beyond the scope of this study, it is possible that a finer-scale examination of individual feeding trees might reveal greater differences if we did not group several different large and productive food trees for this variable. Additionally, examination of the control variables for within-group behaviour (affiliative social and aggression) revealed that both are likely important for overall cohesion. Here we aimed to control for these effects because our focus was on a proxy for overall group spatial cohesion and because each unit of our response variable comprised many different individuals from different positions within a group. Yet, it is likely that more individual-based analyses in many primates would find additional characteristics such as age, rank, or personality characteristics important for cohesion. Interestingly, we found that cohesion seemed to increase when more within-group aggression was recorded. Future studies might attempt to examine how risk from within a social group could affect an individual's decision to remain close to conspecific neighbours. However, as previously noted, if a study species is predated on by human-intolerant carnivores but experiences a "human-shield" while observed, subjects may perceive this change (Nowak et al. 2014). This may mean results could inflate the way in which animals respond to within-group risk because they may face less risk from outside the group. This could also apply to risk from unhabituated groups of the same species. One workaround to this problem could be the use of camera traps for measuring number of neighbours or another proxy for spatial cohesion. For example, McCarthy et al. (2019) were able to use images for creating social networks of party association in wild

chimpanzees which has been typically measured through direct observation. While camera trapping for studying primate social behaviour is relatively new, these methods could offer a solution when direct observation could alter risk (LaBarge et al. 2020).

Behavioural differences between groups are often attributed to group size without accounting for predominant 'personality' types of individuals (individual-level behavioural traits that are repeatable across time) across the group (Keiser and Pruitt, 2014). Thus, these observed differences in absolute number of neighbours might be due to differences in their perception of risk, group composition, or a combination of factors. It should also be noted that while our larger group was approximately double the size of our smaller study group, both were large compared with other studied populations of Sykes monkey (*C. albogularis*) (Cowlishaw et al. 2004) or blue monkey (*Cercopithecus mitis*; previously considered conspecific with samangos) (Cords, 2012). One difference between our two groups was that the Barn group used a smaller total ranging area during the study period (147.15 versus 237.66 hectares for House, Sept. 2015 – Dec. 2017) while encountering a similar number of eagles over the period used to construct the risk landscapes. This could mean that this group needed to be more cohesive during most baseline observations because avoidance of risky locations was more difficult.

Conclusions

Spatial cohesion is important for the stability of animal groups and for effective social information transfer about risks or resources (Evans et al. 2016; Frechette et al. 2014), but local environmental conditions may affect the costs and benefits of remaining near groupmates. Cohesion in samangos is an apparently flexible characteristic which changes reactively to encounters with competing groups but not to immediate predation risk from eagles. Whether this is also true with terrestrial predators is uncertain, but future studies using methods other than direct observation of habituated subjects might be better suited to answer that question.

Our results indicating pre-emptive changes associated with eagle risk suggest that this species might recall attributes of risky locations. This is unsurprising given previous studies finding samangos avoid areas on the landscape where they face greater risk from eagles (Coleman & Hill, 2014). Yet, few studies focused on

animal "landscapes of fear" attempt to infer mechanisms underlying spatial variation in predation avoidance or antipredator behaviours. Future studies might explicitly consider the relative contributions of habitat attributes and the memory of previous encounters using field experiments with cues from predators or competitors.

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TABLES AND FIGURES

Hypothesis	Model	Response	Offset	Fixed Effects	Random Effects
Null	0	Count of Nearest Neighbours	# individuals per scan sample	**Control variables**: Samango Group ID; Habitat structure (canopy cover, understory visibility); Proportion feeding rare/spatially clumped fruiting trees; Within-group aggression and affiliative behaviour	Time of sample x Unique 'Event' ID x Spatial location
Hypothesis 1 (Reactive Changes Only)	1	"	"	Null + Risky 'Events'	"
Hypothesis 1 (Reactive Changes interacted with Habitat Structure)	2	"	"	Null + Risky 'Events' * Habitat Structure	"
Hypothesis 1 + 2 (Combined Reactive + Pre-emptive changes)	3	"	"	Null + Risky 'Events' + Relative Eagle Risk + Relative Inter-group Risk (location-specific)	"
Hypothesis 2 (Pre-emptive Changes Only)	4	"	"	Null + Relative Eagle Risk + Relative Inter-group Encounter Risk	"
Hypothesis 2 (Eagle Risk Only)	5	"	"	Null + Relative Eagle Risk	"
Hypothesis 2 (Inter-group Encounter Risk Only)	6	"	"	Null + Relative Inter-group Encounter Risk	"
Hypothesis 2 (Eagle Risk Interacted with Habitat structure)	7	"	"	Null + Relative Eagle Risk * Habitat Structure	"
Hypothesis 2 (Inter-group Risk Interacted with Habitat Structure)	8	"	"	Null + Relative Inter-group Risk * Habitat Structure	"

Table 1. Candidate models and their components. Response is modelled with an offset to correct for variation in the number of individuals per scan sample.

Model	K	loglik	AICc	Δ_i	ω_i	Ev. Rat	Marginal - Pseudo R^2 %	Conditional - Pseudo R^2 %
1	**19**	**-3794.62**	**7627.91**	**0.00**	**0.57**	**1.00**	**13.59%**	**53.01%**
3	**21**	**-3792.88**	**7628.602**	**0.69**	**0.41**	**2.25**	**14.44%**	**54.06%**
0	11	-3806.63	7637.57	9.64	0.0046	124.41	11.62%	53.03%
5	12	-3806.08	7638.38	10.47	0.0031	188.45	12.63%	54.18%
6	12	-3808.36	7639.05	11.14	0.0022	262.78	11.72%	54.82%
4	13	-3805.77	7639.92	12.01	0.0014	406.34	12.37%	54.03%
7	14	-3807.89	7640.06	12.15	0.0013	436.07	12.73%	53.76%
8	14	-3806.65	7641.68	13.77	0.0006	977.68	11.92%	53.17%
2	35	-3788.08	7648.46	20.55	0.0000	29020	14.61%	53.48%

Table 2. Model selection criteria and models ranked by weight and evidence ratios. Potential top models (1, 3) had a Δ_i of less than 6 and the null. All models contained the random effects and the fixed effects of group, proportion of sampled individuals engaged in social behaviour and the number of within-group aggressions that have occurred up to that time point. K represents the number of parameters; logLik is the log-likelihood; AICc is the small-sample corrected Akaike Information Criterion; Δ_i is the change in AICc; ω_i is the model weight; Ev. Rat. is the evidence ratio calculated by dividing the model with the highest weight by the weight of the candidate model
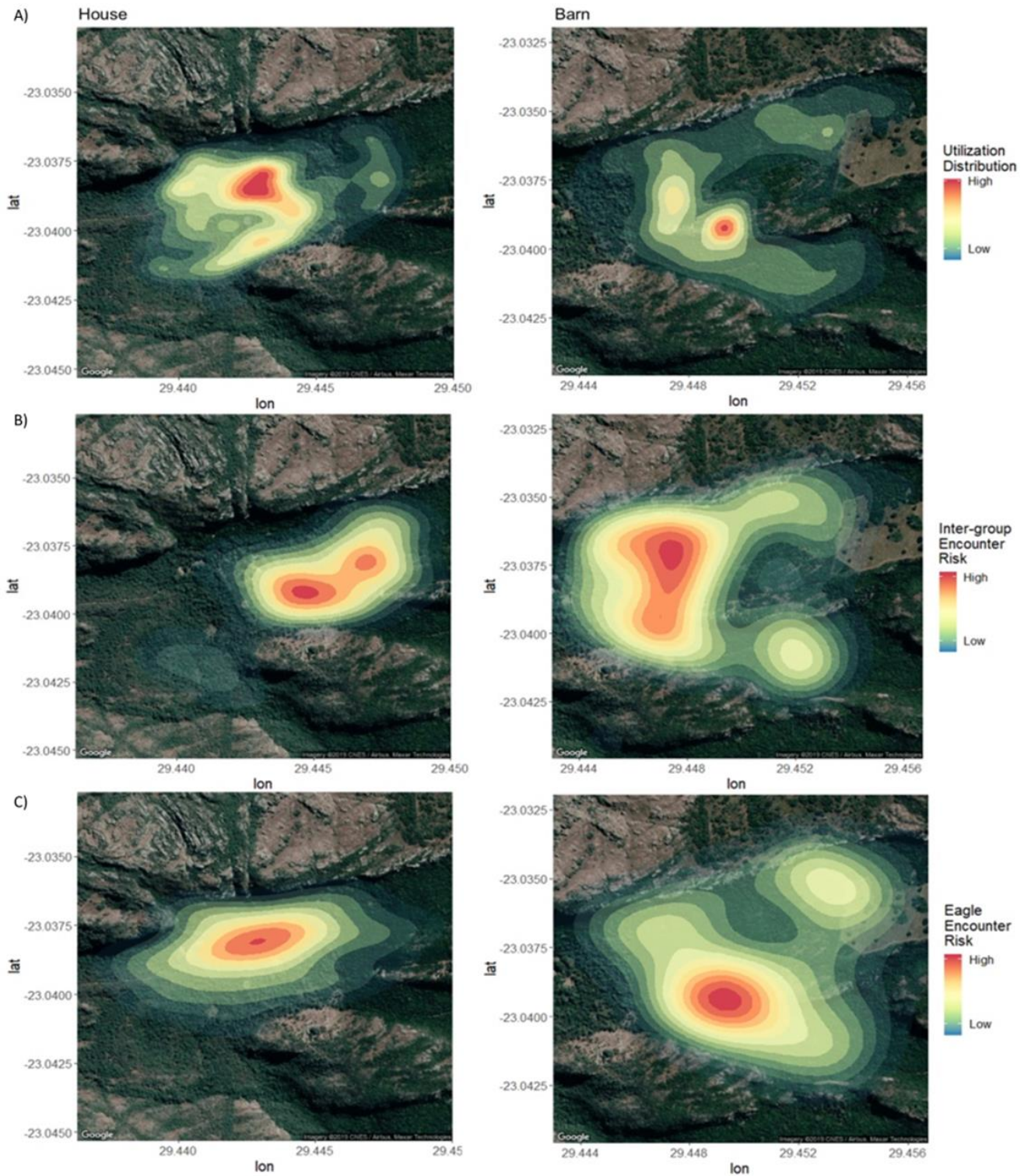
Figure 1. (A) Utilization distribution (100%) for the two groups based on frequency of GPS points recorded prior to all scan samples collected for the 12 months preceding each sample. (B) Eagle Risk for the two groups based on frequency of encounters (n=67 for Barn and n=61 for House) that were used to create relative risk values based on kernel density estimation. (C) Inter-group encounter risk. Colours represent relative values (n=205 for Barn and n=92 for House). Rasters created for calculating relative risk were updated monthly with points from the previous 12 months and were converted to UTM and corrected for overall utilization.
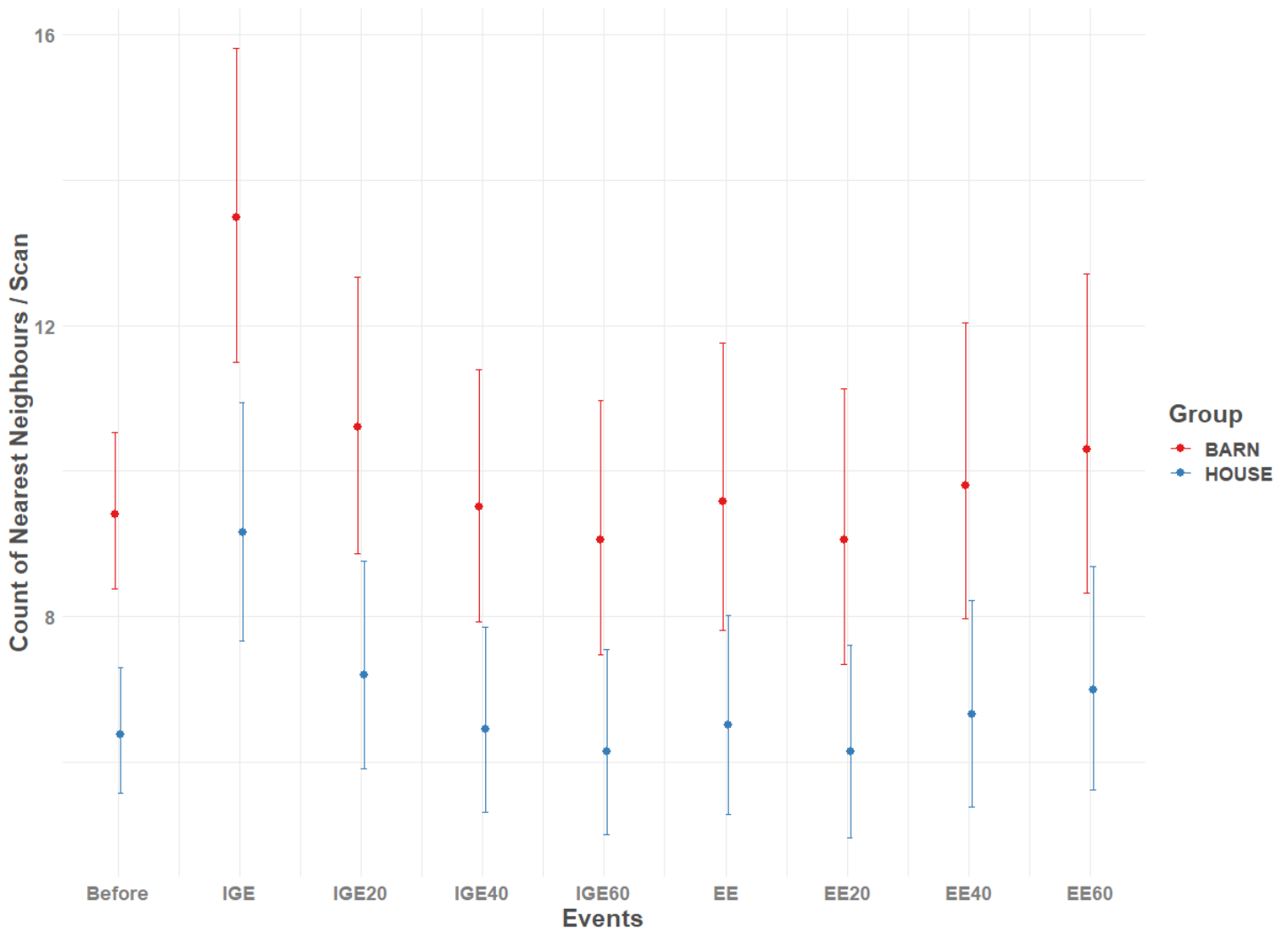
Figure 2. Counts of nearest neighbours per scan sample for both groups for baseline observations, inter-group encounters (IGE) and eagle (EE) and for behavioural samples collected 20, 40, and 60 following each type of event. This calculation holds the total number of individuals sampled constant at its mean. Both groups tended to be more cohesive during inter-group encounters (n=45 for House and n=99 for Barn). We sampled individuals within the House group as having fewer neighbours than the Barn group. Eagle encounters (n=40 for House and n=34 for Barn) did not apparently elicit a change in neighbours compared to baseline levels. Fitted counts are based on marginal averages from model 3. Bars represent 95% prediction intervals.
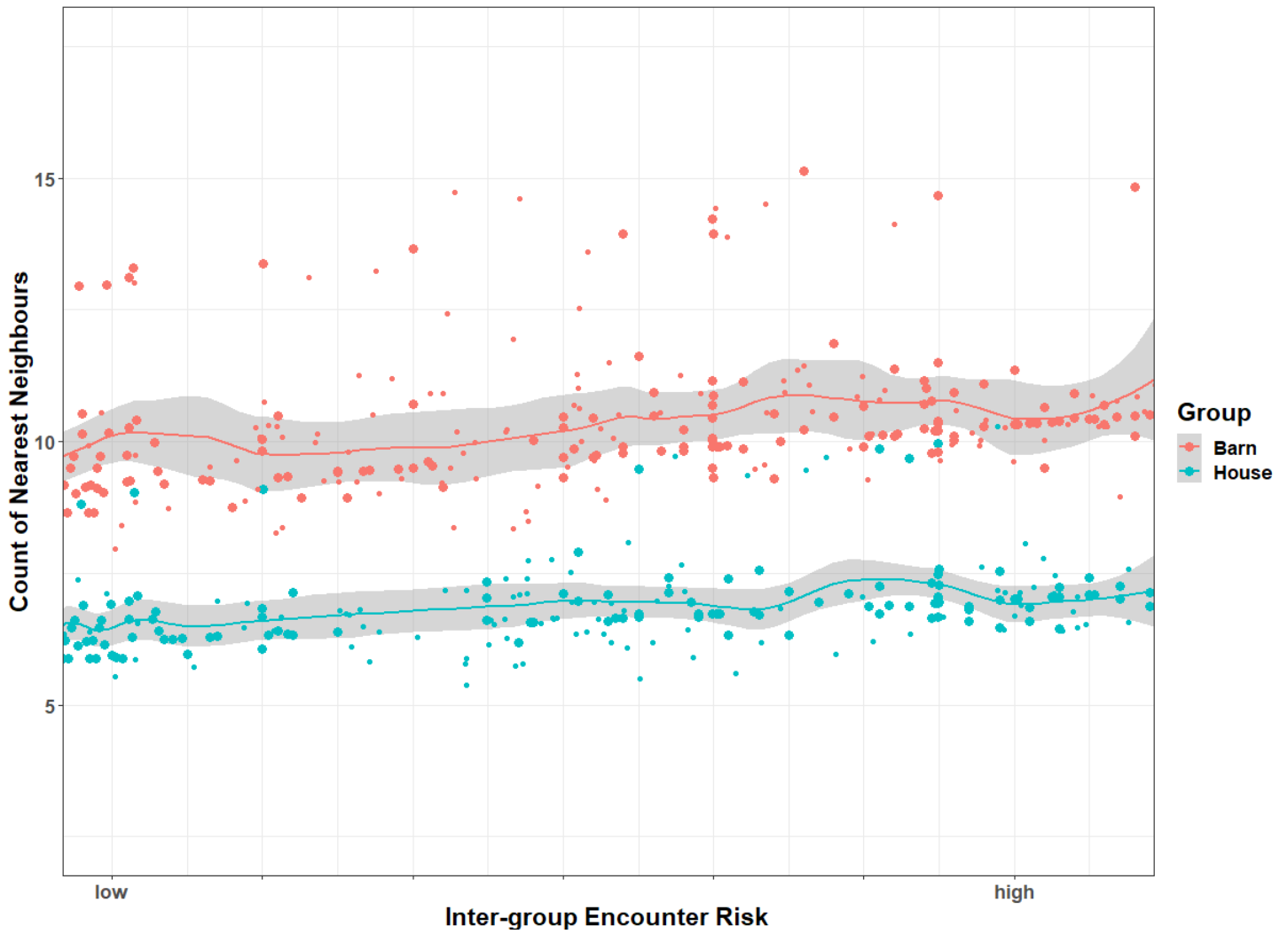
Figure 3. Predicted counts of neighbours under varying inter-group encounter risk based on model 3. Both groups showed little increase in cohesion over baseline values, even in areas of highest risk. Line represents the mean and surrounding shaded areas represent 95% prediction intervals of the mean.
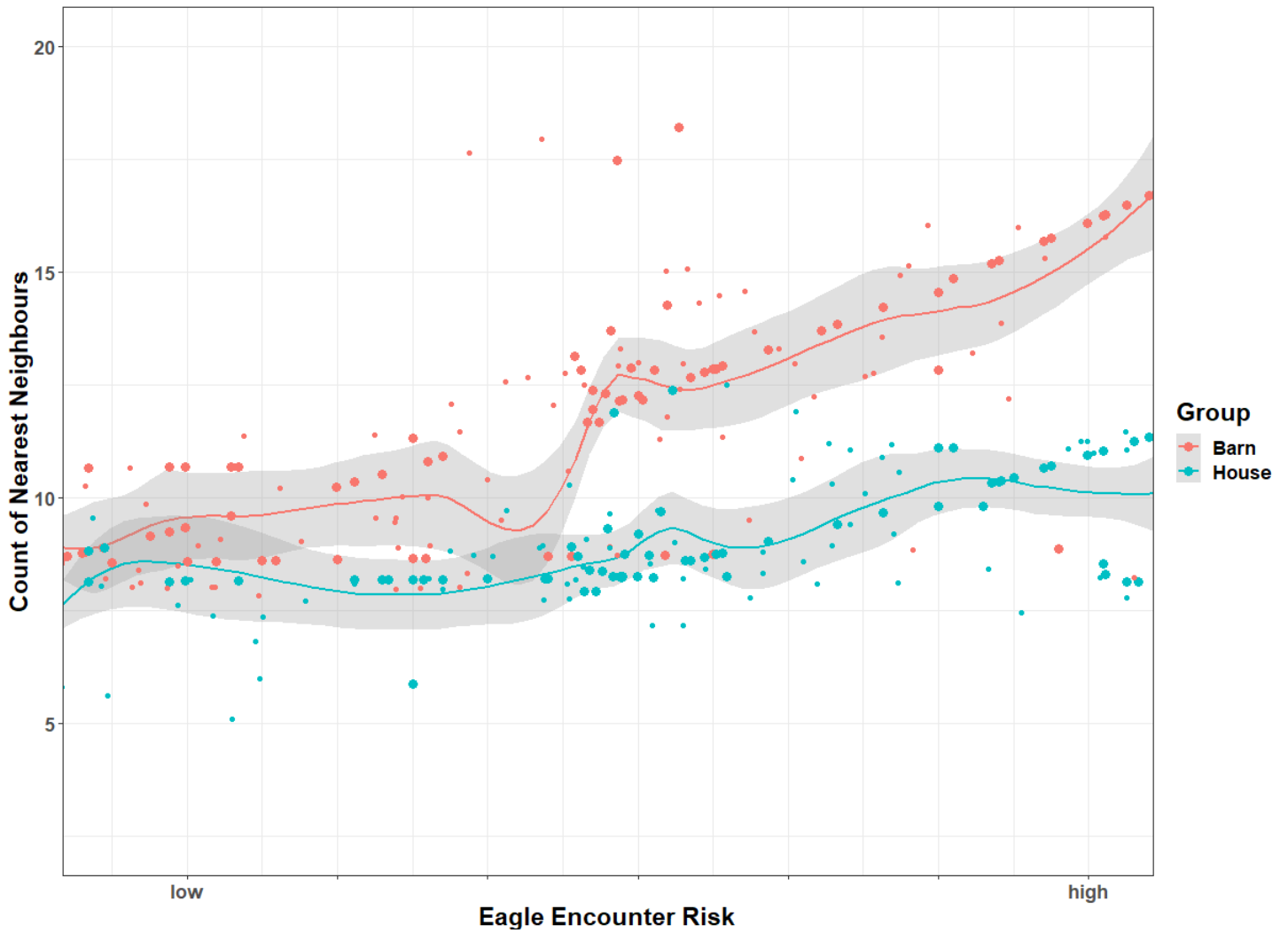
Figure 4. Predicted Counts of neighbours under varying eagle encounter risk based on model 3. Both groups tended to be more cohesive under heightened eagle risk, but this effect was stronger for Barn versus House group. Line represents the mean value and surrounding area is its 95% prediction interval.