Using social networks to explore the social flexibility of urban vervet monkeys

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Abstract

Increasing urbanisation reduces available habitat and increases human-wildlife interactions, presenting social and ecological challenges for many species; however, flexible generalist species, such as the vervet monkey, *Chlorocebus pygerythrus*, thrive under these pressures. In the urban mosaic, human-food sources represent clumped, monopolisable food that can increase contest competition. Social network analysis (SNA) is a powerful tool to monitor changes in social structure, yet it has rarely been used to study urban wildlife. Using SNA, we investigated the effect of anthropogenic food and human-wildlife interactions on social cohesion in five vervet monkey groups in urban KwaZulu-Natal, South Africa. Over six months, we conducted group scan samples every 30-min on each group and recorded all humans-vervet monkey interactions during dawn to dusk follows. We analysed the effect of foraging on natural and human-related food sources and human-vervet monkey interactions on social network metrics for grooming and aggression at group (density, clustering coefficient and distance) and individual (eigenvector centrality and degree) levels, using linear mixed models. Anthropogenic food influenced almost all social metrics. At the group level, foraging on anthropogenic food was related to increased density and cohesion in both grooming and aggression networks. At the individual level, increasing anthropogenic food affected high-ranking monkeys most: eigenvector centrality and outdegree in aggression networks increased with rank. Social network analysis can be a useful tool to document urban effects on wildlife groups, and aids our understanding of wildlife behavioural flexibility, a key tool in developing educated and effective management strategies.

Keywords Socio-ecology · Human-wildlife coexistence · Anthropogenic food · Chlorocebus pygerythrus · Ethnoprimatology

Introduction

The urban mosaic landscape is widely acknowledged as an important ecological system (Downs et al. 2021), yet our understanding of social adaptations within this ecological

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system is relatively limited (Lacy and Martins 2003; Thatcher et al. 2023). Evidence is accumulating that social network positions have fitness consequences that impact population dynamics (e.g. Royle et al. 2012), and therefore, an animal's social network is expected to respond flexibly to environmental change (Snijders et al. 2017). Behavioural traits can affect effective population size through reproductive skew (Anthony and Blumstein 2000), and thus, increasing understanding of social behavioural processes can inform and contribute to wildlife conservation management.

Although research into anthropogenic wildlife social networks is steadily growing (e.g. elephants, *Elephas maximus*, Chiyo et al. 2012; moor macaques, *Macaca maura*, Morrow et al. 2019; spotted hyenas, *Crocuta Crocuta*, Belton et al. 2018; giraffes, *Giraffa camelopardalis,* Bond et al. 2021; bottlenose dolphins, *Tursiops aduncus*, Chilvers and Corkeron 2001), there are few assessments of peri-urban species (e.g. *Macaca* spp. Balasubramaniam et al. 2020; Balasubramaniam et al. 2021a, b; Chakraborty et al. 2023), and even fewer on urban species (e.g. domesticated dogs *Canis lupus familiaris*,

Bhattacharjee and Bhadra 2020; sulphur-crested cockatoos, *Cacatua galerita*, Aplin et al. 2021). Understanding the interaction between anthropogenic food and ecological factors on social dynamics is important to developing our understanding of wildlife flexibility in the urban landscape (McKinney 2015; Balasubramaniam et al. 2021a, b), particularly in primate species (Thatcher et al. 2023).

Feeding competition is one of the most fundamental factors affecting fitness in animals (Chapman et al. 2012). Understanding how the distribution of food resources influences the nature of feeding competition is a central feature of ecological explanations of social structure and organisation (e.g. Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Isbell and Young 2002). Changes in landscape profiles caused by anthropogenic pressures directly influence food distribution and availability, altering ecological and social challenges for many species (Chilvers and Corkeron 2001; Gilchrist and Otali 2002; Prange et al. 2011; Chakraborty et al. 2023). Anthropogenic suburbs provide habitats that are productive and well maintained, providing abundant dispersed resources (McKinney 2002), particularly in selectively maintained gate communities (Ballard and Jones 2011; Alexander et al. 2019a, b, c, 2021). Furthermore, anthropogenic environments also bring benefits such as increased access to high-value, patchy, monopolisable human food resources. Socioecological theory predicts that high-value monopolisable resource distribution gives rise to strong within-group contest competition (WGC) and when coupled with low between-group contest competition, should create more cohesive groups (Wrangham 1980; Sterck et al. 1997; van Schaik and Van Noordwijk 1998). Within such groups, small, supportive networks should form with key central individuals (van Schaik 1989), a more linear despotic hierarchy should be apparent, and females should form frequent coalitions to maintain rank-related benefits (Isbell 1991a, b; Sterck et al. 1997; Isbell and Young 2002). The effect of such ecological pressures on social structure has not yet been applied to intragroup variation in urban wildlife; nevertheless, using the rationale of WGC to test these ecological pressures allows a greater understanding of both group and individual adaptations to urbanisation.

Behavioural flexibility has desirable fitness benefits within the urban ecosystem (Sol et al. 2013), particularly for adaptive generalist species such as the vervet monkey, *Chlorocebus pygerythrus* (Chapman et al. 2016). Vervet monkeys are a highly social species that live in multimale-multifemale groups, are female philopatric and have strict female and male dominance hierarchies (e.g. Seyfarth and Cheney 1984; Borgeaud and Bshary 2015). They are highly adapted to an urban landscape (Saj et al. 2001; Patterson et al. 2017, 2018) and exhibit behavioural flexibility in response to anthropogenic disturbance (Chapman et al. 2016). Grooming and aggression are common behaviours among non-human primates (hereafter primates)

that reflect cooperation and competition, respectively (Sueur et al. 2011) and are therefore, key metrics for social network analysis in primates. Previous social network studies have shown the strong influence of female philopatry and rank on vervet monkey social metrics (Henzi et al. 2013; Josephs et al. 2016; Young et al. 2017; Borgeaud et al. 2017). Vervet monkeys, therefore, provide a suitable model to test social flexibility in an urban matrix.

In our study, vervet monkeys had an abundant dispersed supply of natural food through the selectively maintained gardens and natural areas within their urban home range, whereas high-value human food was obtained by entering homes or raiding refuse (Thatcher, pers. obs.); these human foods were therefore opportunistic and clumped. Based on socioecological theory, we expected that greater exploitation of these high-value human foods and less dependence on natural food resources would increase WGC. We, therefore, made a group-level prediction: (*1a*) groups that foraged on these clumped human food resources more frequently would increase their grooming connections and aggressive interactions; thus, network density (both grooming and aggression) should increase, and distance should decrease compared with those that fed primarily on natural food resources, as group-living animals can adopt multiple competitive foraging strategies (Isbell et al. 1991). We further predicted (*1b*) that an increase in differentiated relationships should lead to increased sub-grouping. At the individual level, we predicted that (*2a*) because of the strict linear hierarchy associated with increased WGC, higher-ranked individuals would obtain more anthropogenic food and, therefore, be more central within their group grooming and aggression networks. Finally, because of female philopatry in vervet monkeys, we predicted that (*2b*) females would receive more grooming and aggression than males and be more central. We made no specific predictions about human aggression (e.g. chasing, or throwing of rocks); however, we included it as an additional level of anthropogenic disturbance to human food consumption.

Methods

Subjects and study site

We studied five groups of urban vervet monkeys (Table 1) in Simbithi Eco-estate, Ballito, Durban North-coast, KwaZulu-Natal, South Africa (S:29.3029, E:31.131). Simbithi Eco-estate is a gated housing estate converted from sugar cane farms to create a complex urban mosaic of urban built and green spaces (natural and managed) (Alexander et al. 2019a, b, c, 2021). The estate comprises a variety of urban complexes, structures and housing options, along with areas of human-made coastal forest and managed walking trails (Alexander et al. 2019a, b, c, 2021).

Table 1 Urban vervet monkey group composition, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa

Group	Males	Females	Juveniles	Total
Balito	3	5	5	14
Farmyard	4	10	9	23
Savannah	4	10	11	25
Goodies	5	10	14	29
Herron	5	14	23	42

We habituated all groups to the presence of one observer at close proximity (10 m) over a two-month period, six months before data were collected. A group was deemed habituated when the observer could approach within 10 m proximity with no flight response.

We conducted our study from September 2016- February 2017. We studied only adult vervet monkeys, and all were individually recognisable from distinct markings. No population genetic data was available. The study period did not include the dispersal and mating seasons (April-July); therefore, the numbers of adults across groups were relatively stable. We collected data during the austral spring (September–October) and summer (November-March) in KwaZulu-Natal (SANBI 2017).

Behavioural data collection

HT collected vervet monkey behaviour data from dawn until dusk (~ 12 h in spring and ~ 17 h in summer). We conducted instantaneous group scans every 30 min for a 10-min period, recording both grooming and aggressive interactions, including the identity of the social partner/s. We also noted the occurrence of any dominance interactions and aggressive competition ad libitum. We collected all data using the Prim8 behavioural software (McDonald and Johnson 2014) on a handheld Lenovo tablet. We only present data on intragroup conflict, as our intergroup encounter rate was very low.

We used all occurrence sampling to record all interactions between humans and vervet monkeys during our dawn to dusk daily follows. We defined a human-related incident as any occasion when at least one vervet monkey interacted with humans directly or human-related possessions (e.g. houses, bins and cars). We classified incidents as positive (raiding, provisioning) or negative (human aggression towards monkeys). For positive human incidents, we included any form of human food consumption; human food consumption was considered a new event if the monkeys had not raided or been fed for the previous 20 min. We classed negative human incidents as any form of human-monkey aggression, independent of who initiated the attack. We recorded an incident as terminated once all parties were no longer in sight of each other, and recorded a new incident if

there had been no human-monkey aggression in the previous 20 min. We recorded natural food consumption using focal animal sampling, noting all events when a monkey was seen consuming natural food following standard classification of foraging behaviour (Saj et al. 1999).

Association measures

We constructed directed weighted matrices for grooming and aggression per month. We calculated measures of network structure using UCInet (Borgatti et al. 2002). We used three commonly used network parameters to quantify group-level social associations: density, distance and a clustering coefficient (Croft et al. 2008) that could test overall connectedness and degree of sub-grouping within the group. Density is a measure of dyadic connections (ties) in a population with respect to the potential number of ties and reflects overall group cohesion. We expressed this as a percentage of social association: high scores represented a saturated network while low scores indicated a sparse network. We further assessed distance as a measure of direct social interaction. Distance reflects the shortest path of connections between two individuals and so, distance increases as networks become less cohesive. We calculated the average distance between pairs within a network, allowing us to assess how well connected a group was. The global clustering coefficient reflects the level of sub-grouping within the group, and measures how clustered a network is, e.g. how many 'cliques' are in a network.

We used three common network parameters to assess individual metrics: eigenvector centrality and degree centrality (Croft et al. 2008). Eigenvector centrality reflects an individual's connection to other well-connected individuals (Croft et al. 2008), and has been found to be a better predictor of fitness than the strength of a relationship (Cheney 2016). Degree measures how many direct ties or relationships an individual has; an individual with more ties has higher centrality and thus, is a basic measure of connectedness. Outdegree refers to the number of ties originating from the focal (e.g. grooming given) whilst in-degree is the number of ties directed at the focal (e.g. grooming received). It is possible for individuals ro have the same number of ties (degree) but different eigenvector centrality because the connectedness of their partners to few or many others may vary. We used a weighted matrix to calculate eigenvector centrality and a binary matrix to assess degree. Again, we assessed both grooming and aggressive associations.

Statistical analyses

We conducted all statistical analyses using the R statistics programme (R Project 2013). We calculated a monthly rate (frequency/hour) for the two human incident measures

(positive and negative) and natural food consumption. For brevity, we hereafter refer to the latter variable as natural food. We calculated both a group level and individual frequency for separate analyses of our individual and group level prediction. We assessed dominance rank monthly for each vervet monkey group as a combined male–female hierarchy. Although we acknowledge the value of Elo-ratings as a measure of rank overtime (Albers and de Vries 2001; Neumann et al. 2011), we also acknowledge the advantages of David's score to allow a stronger comparison between individuals at a given time (Gammell et al. 2003; De Vries et al. 2006) and therefore used David's score as a measure of rank in this study. David's score measures the success of an individual winning relative to their opponents, hence providing a comparative measure of competitive ability. We calculated a normalised David's score rank using the Steepness package (Leiva and de Vries 2011) in R.

Social network data is inherently non-independent because of the interconnectedness between individuals within the network. Whilst there are several options for analysing network data, recent research has demonstrated the benefit of using mixed effect models that address interdependence in the data and control for the effects of actor and receiver (Hart et al. 2022).

We created 12 linear mixed models (LMM) in total using the *lme4* package (Bates 2010), with each social metric as the dependent variable. We created three models for our group metrics and three models for our individual metric models, and we ran these for aggression and grooming behaviours. Within each model, each row represented a mean monthly social metric calculated per group/individual. We constructed two separate model structures for group and individual metrics to address our questions separately. To test Predictions 1 and 2, we included predictor variables to reflect human-food resources (positive human incidents) and natural food resources, and because group size is known to affect intragroup contest competition in primates (e.g. Balasubramaniam et al. 2014) we included the number of adults in each group (group size). We ran an interaction between positive human incidents (clumped) and

natural food (dispersed) to assess our group-level prediction of clumped food increasing WGC. To test our individual-level prediction, we additionally added sex and rank as predictors and ran an interaction between positive human incidents with sex and rank separately to assess the effect of linear hierarchy and WGC. Finally, we included negative human incidents (human-vervet monkey aggression) in all models as we previously found this factor affected time spent foraging in these groups (Thatcher et al. 2020).

Group level prediction

Group social metric ~ positive human incidents*natural food + negative human incidents + group size + (1|group identity).

Individual level prediction

Individual social metric ~ sex*positive human incidents + rank*positive human incidents + negative human incidents + natural food + group size + (1|group identity/monkey identity).

We used the *boot* package (Davison and Hinkley 1997; Canty and Ripley 2017) in R to run our models and bootstrap the confidence intervals of our model parameters to further avoid assumptions about the distribution from which the data were obtained. As we recorded active affiliative behaviours, we chose to run permutations on our parametric models (Hart et al. 2022) and ran all models using 1000 permutations. If the upper and lower CI straddled 0, then we did not consider the effect significant. We assessed the fit of each model graphically, checking residuals for normal distribution.

Results

We observed each vervet monkey group for a minimum of 4 days and a maximuim of 6 days a month (mean 4.53 ± 0.63 (SD)). Over 6 months, we collected a mean ($\pm$ SD) of

Fig. 1 Example sociogram representing the Ballito vervet monkey troop. (Note: Black circles represent female monkeys, and white squares represent male monkeys. The networks have been spring-embedded). Networks represent two separate months, where (**a**) is the month with the highest rate of positive human incidents and (**b**) is the month with the lowest positive human incidents
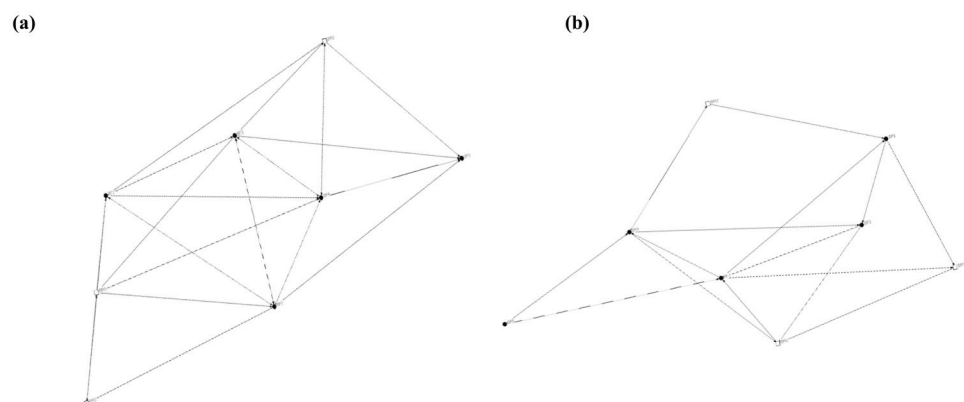
(a)

(b)

Table 2 Summary of significant effects from the LMM for the group level predictions for both grooming and aggression. We present both our predicted outcome and significant results where confidence intervals did not straddle 0 and + and—signs show the directionality of the effect

		Positive human incidents		Positive human incidents* Natural food	
		Predicted	Result	Predicted	Result
Grooming	Density	+	+	+	+
	Clustering	+	+	+	
	Distance	-	-	-	-
Aggression	Density	+	+	+	+
	Clustering	+	+	+	
	Distance	-	-	-	

315 ± 25.34 scans per group with a monthly average of 52.5 ± 7.0. Networks showed clear variation between vervet monkey troop social metrics. We found consistent effects of positive human incidents increasing group cohesion and centrality measures (Fig. 1, Table 2 and 3).

Group level predictions

Group Prediction 1a We found a positive interaction effect between natural food and positive human incidents on grooming density, supporting the group-level prediction *1a*

for grooming. When the rate of positive human incidents and natural food was low, grooming density increased; however, this was offset by an increased rate of natural food decreasing grooming density (Table 3, Fig. 2a). Supportive to this, we found a negative interaction effect on distance (Table 3, Fig. 2b); distance decreased with an increased rate of positive human incidents, however as natural food availability increased distance plateaued. Aggression metrics also met our group-level prediction 1a, as we found that a greater rate of positive human incidents was significantly related to decreased distance within the network. Furthermore, we found a significant positive interaction between positive human incidents and natural food for the aggression network density. Increased frequency of positive human incidents was associated with a sharp increase in density, however, when the rate of natural food increased, density significantly decreased (Table 4, Fig. 2c).

Group Prediction 1b The clustering coefficient did not show a significant interaction. However, an increased clustering coefficient for both grooming (Table 2) and aggression (Table 3) were positively related to a higher rate of positive human incidents, supporting group-level prediction *1b* for grooming.

Individual level predictions

We found partial support for our individual-level predictions (Table 5).

Table 3 The LMM output and bootstrapped confidence intervals for group-level grooming social metrics of urban vervet monkeys, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa. (Bold text highlights significant results)

|	Effect	Estimate	Standard error	CI lower	CI upper
Density (R^2 marginal: 0.81; R^2 conditional: 0.90)	(Intercept)	1.63	0.19	1.26	2.01
	Negative human incidents	-0.02	0.08	-0.18	0.13
	Positive human incidents	0.63	0.11	-0.42	-0.04
	Natural food	-0.40	0.18	0.06	0.76
	Group size	-0.33	0.17	-0.71	0.01
	Positive human incidents* Natural food	**0.26**	**0.13**	**-0.51**	**-0.02**
Clustering coefficient (R^2 marginal: 0.52; R^2 conditional: 0.69)	(Intercept)	0.28	0.04	0.23	0.74
	Negative human incidents	-0.01	0.01	-0.03	0.02
	Positive human incidents	**0.13**	**0.02**	**-0.02**	**-0.58**
	Natural food	-0.06	0.03	-0.08	0.03
	Group size	0.05	0.03	-0.148	0.07
	Positive human incidents* Natural food	-0.01	0.00	0.05	-0.03
Distance (R^2 marginal: 0.85; R^2 conditional: 0.92)	(Intercept)	2.58	0.33	1.93	3.24
	Negative human incidents	-0.07	0.13	-0.36	0.19
	Positive human incidents	-0.18	0.20	-3.82	-4.20
	Natural food	-0.44	0.31	-1.05	0.17
	Group size	0.36	0.28	-0.25	0.94
	Positive human incidents* Natural food	**-0.11**	**0.12**	**0.23**	**0.04**
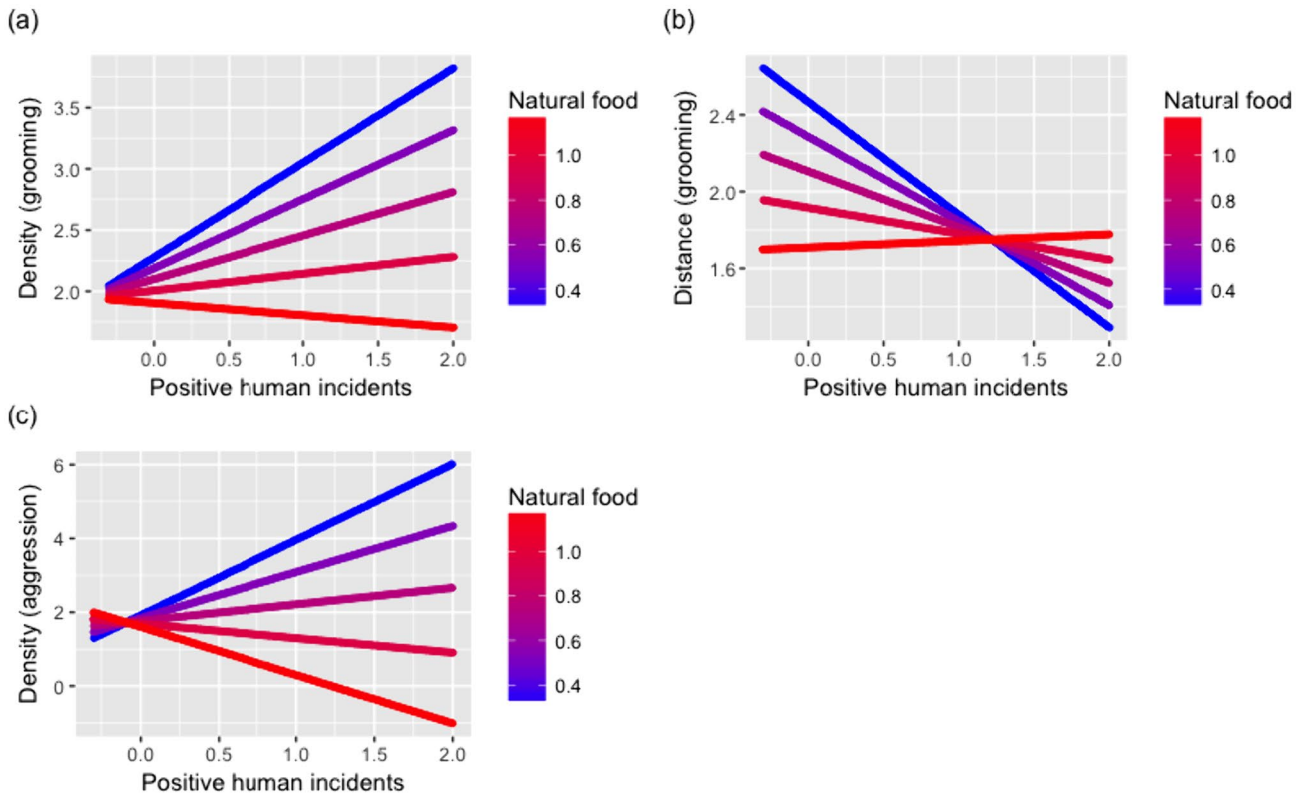
Fig. 2 Interaction between group natural food rate per hour and group positive human incidents rate per hour on group level social metrics of urban vervet monkeys at Simbithi Eco-estate, North Durban, KwaZulu-Natal, South Africa, where a) shows the positive effect on grooming density, b) shows the negative effect on grooming distance and c) shows the positive effect on aggression density

Table 4 The LMM output and bootstrapped confidence intervals for group-level aggression social metrics of urban vervet monkeys, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa. (Bold text highlights significant results)

	Effect	Estimate	Standard error	CI lower	CI upper
Density (R^2 marginal: 0.70; R^2 conditional: 0.89)	(Intercept)	0.29	0.16	0.77	1.37
	Negative human incidents	0.06	0.01	-0.02	0.01
	Positive human incidents	0.12	0.01	0.11	0.04
	Natural food	-0.04	0.02	0.01	0.09
	Group size	0.00	0.01	-0.02	0.00
	Positive human incidents* Natural food	**0.14**	**0.00**	**0.13**	**0.21**
Clustering coefficient (R^2 marginal: 0.68; R^2 conditional: 0.88)	(Intercept)	0.28	0.04	0.21	0.36
	Negative human incidents	-0.01	0.01	-0.04	0.02
	Positive human incidents	**0.07**	**0.02**	**0.02**	**0.11**
	Natural food	-0.06	0.03	-0.13	0.01
	Group size	0.05	0.03	-0.02	0.13
	Positive human incidents* Negative human incidents	-0.04	0.02	-0.08	0.01
Distance (R^2 marginal: 0.90; R^2 conditional: 0.91)	(Intercept)	0.70	0.43	-0.49	0.33
	Negative human incidents	0.01	0.03	-0.02	0.47
	Positive human incidents	**-0.09**	**0.04**	**-0.21**	**-0.73**
	Natural food	0.00	0.00	-0.32	0.47
	Group size	**0.08**	**0.01**	**0.27**	**1.10**
	Positive human incidents* Natural food	0.00	0.00	-0.22	0.14
	Positive human incidents* Negative human incidents	-0.02	0.00	-0.48	0.01

Table 5 Summary of significant effects from the LMM for the individual level predictions for both grooming and aggression. We present both our predicted outcome and significant results where confidence intervals did not straddle 0 and + and—signs show the directionality of the effect

		Positive human incidents		Sex		Rank		Positive human incidents* Rank	
		Predicted	Result	Predicted	Result	Predicted	Result	Predicted	Result
Grooming	Eigenvector	+	+	♀	♀	+		+	
	Indegree	+		♀	♀	+		+	-
	Outdegree	+		♀	♀	+		+	
Aggression	Eigenvector	+		♀		+		+	+
	Indegree	+		♀		+		+	
	Outdegree	+	+	♀		+		+	+

Individual Prediction 2a At the individual level, prediction *2a* was partially met for our grooming and aggression metrics (Table 6 and 7). Unexpectedly, we found a significant negative interaction between positive human incidents and rank for grooming indegree. Individuals' grooming indegree increased with rank when rates of positive human incidents were low, however, as the rate of positive human incidents increased grooming indegree increased across ranks (Table 6, Fig. 3a). We found a positive interaction between positive human

incidents and rank for both aggression eigenvector centrality and aggression outdegree (Table 7, Fig. 3b, c). When positive human incidents were high, higher-ranking monkeys' aggressive connectedness (eigenvector centrality) increased; however, when positive human incidents were low, aggressive connectedness (eigenvector centrality) decreased. When the rate of positive human incidents increased, aggression outdegree increased with rank; however, when the rate of positive human incidents was low, the effect of rank weakened (Table 7).

Table 6 The LMM output and bootstrapped confidence intervals for individual level grooming social metrics of urban vervet monkeys, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa. (Bold text highlights significant results)

	Effect	Estimate	Standard error	CI lower	CI upper
Eigenvector centrality (R^2 marginal: 0.29; R^2 conditional: 0.51)	(Intercept)	0.29	0.03	0.20	0.34
	Positive human incidents	**0.06**	**0.02**	**0.02**	**0.12**
	Negative human incidents	**0.01**	**0.01**	**-0.06**	**-0.02**
	Natural food	0.01	0.01	-0.01	0.02
	Group size	**-0.05**	**0.01**	**-0.09**	**-0.03**
	Rank	0.00	0.01	-0.01	0.02
	Sex	**-0.15**	**0.03**	**-0.20**	**-0.07**
	Rank*Positive human incidents	0.00	0.01	-0.01	0.01
	Sex*Positive human incidents	0.01	0.02	-0.02	0.06
Indegree (R^2 marginal: 0.37; R^2 conditional: 0.84)	(Intercept)	23.11	2.39	18.67	28.52
	Positive human incidents	0.42	0.81	-0.93	2.02
	Negative human incidents	**-0.88**	**0.31**	**-1.26**	**-0.02**
	Natural food	-0.12	0.26	-0.26	0.42
	Group size	-1.15	1.08	-2.31	1.29
	Rank	0.13	0.30	-0.68	0.66
	Sex	**-14.81**	**2.04**	**-19.00**	**-11.21**
	Rank*Positive human incidents	**-2.53**	**0.20**	**0.14**	**0.92**
	Sex*Positive human incidents	1.09	0.78	-0.42	2.01
Outdegree (R^2 marginal: 0.27; R^2 conditional: 0.92)	(Intercept)	23.29	2.96	16.51	28.64
	Positive human incidents	0.19	0.69	-2.53	0.22
	Negative human incidents	**-0.04**	**0.27**	**0.05**	**1.24**
	Natural food	**-0.39**	**0.21**	**-0.77**	**-0.04**
	Group size	-0.33	0.99	-1.25	2.17
	Rank	0.05	0.27	-0.53	0.86
	Sex	**-12.79**	**2.40**	**-17.29**	**-7.83**
	Rank*Positive human incidents	-0.20	0.17	-0.25	0.46
	Sex*Positive human incidents	0.40	0.66	-0.67	1.57

Table 7 The LMM output and bootstrapped confidence intervals for individual level aggression social metrics of urban vervet monkeys, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa. (Bold text highlights significant results)

	Effect	Estimate	Standard error	CI lower	CI upper
Eigenvector centrality (R^2 marginal: 0.11; R^2 conditional: 0.69)	(Intercept)	0.20	0.03	0.15	0.30
	Positive human incidents	0.00	0.02	-0.02	0.06
	Negative human incidents	**0.01**	**0.01**	**-0.05**	**-0.02**
	Natural food	0.00	0.01	-0.01	0.02
	Group size	-0.02	0.02	-0.05	0.02
	Rank	0.01	6.57	-0.01	0.02
	Sex	0.04	0.04	-0.05	0.12
	Rank*Positive human incidents	**0.08**	**0.00**	**0.00**	**0.02**
	Sex*Positive human incidents	-0.01	0.02	-0.05	0.02
Indegree (R^2 marginal: 0.24; R^2 conditional: 0.98)	(Intercept)	5.03	1.67	1.95	8.52
	Positive human incidents	0.05	0.21	-0.63	0.29
	Negative human incidents	**0.26**	**0.08**	**0.10**	**0.51**
	Natural food	0.04	0.06	-0.08	0.17
	Group size	0.21	0.32	-0.42	0.79
	Rank	0.08	0.09	-0.25	0.26
	Sex	-0.79	1.24	-3.32	1.51
	Rank*Positive human incidents	0.01	0.05	-0.08	0.16
	Sex*Positive human incidents	-0.17	0.21	-0.54	0.23
Outdegree (R^2 marginal: 0.25; R^2 conditional: 0.80)	(Intercept)	5.21	1.78	2.12	9.73
	Positive human incidents	1.50	0.56	0.39	2.96
	Negative human incidents	**1.05**	**0.23**	**-1.87**	**-0.75**
	Natural food	0.23	0.18	-0.06	0.64
	Group size	-1.18	0.80	-2.68	0.54
	Rank	0.09	0.19	-0.51	0.38
	Sex	1.33	1.03	-0.90	3.44
	Rank*Positive human incidents	**1.31**	**0.13**	**0.08**	**0.68**
	Sex*Positive human incidents	0.68	0.53	-1.72	0.30

Individual Prediction 2b In support of individual level prediction **2b**, we found that females were significantly more central than males for all three measures of grooming centrality (Table 6); however, we found no differences between sex for aggressive metrics (Table 7).

Individual metrics and negative human incidents

Although we made no predictions for negative human incidents, we found that negative human incidents significantly affected all vervet monkey individual metrics, but no group metrics. A higher rate of negative human incidents significantly positively affected all three aggressive centrality measures (Table 6). Increased rates of negative human incidents had a positive significant effect on the grooming eigenvector centrality score; however, they had a negative significant effect on indegree and outdegree (Table 7).

Discussion

All social metrics, both group and individual, appeared to be influenced by either positive or negative aspects of urban living. We present data on intragroup associations only, as intergroup encounters were relatively rare, indicating aggressive intergroup competition was low.

Group level predictions

In support of Prediction **1a**, all group-level metrics were influenced by the rate of clumped human food consumption, and in some cases, this was modulated by the interaction with dispersed natural food consumption. This interaction positively affected both grooming and aggression network density and, as expected, had a negative effect on grooming network distance. More connected networks typically show increased density and decreased distance. This suggests that when human
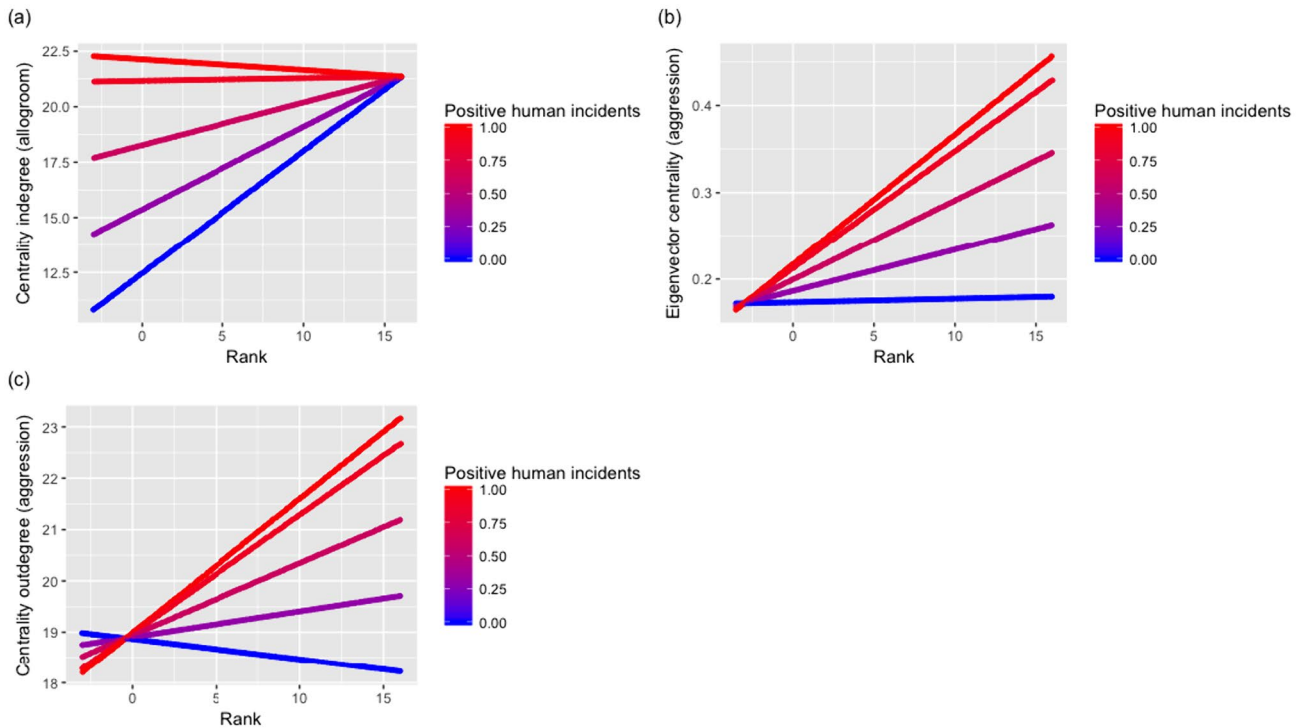
Fig. 3 Interaction between rank (normalised David's score) and individual positive human incidents rate per hour on individual level social metrics of urban vervet monkeys at Simbithi Eco-estate, North Durban, KwaZulu-Natal, South Africa. Where **a**) shows the negative effect on grooming indegree, **b**) shows the positive effect on aggressive eigenvector centrality, and **c**) shows the positive effect on aggressive centrality outdegree

food consumption was high, aggressive competition within the group increased and grooming connections also increased. These findings support established socioecological theories of alliance support over a clumped resource (van Schaik 1989; Hockings et al. 2012). This could also suggest that consuming human-derived food allows vervet monkeys to meet their daily energy requirements more efficiently and therefore have more time available to participate in grooming (Thatcher et al. 2019).

We also found a main effect of positive human incidents on the clustering coefficient in both grooming and aggression networks, indicating that increasing human food consumption increased sub-group formation, supporting our group-level prediction *1b*. It is possible that increasing clique formation is beneficial to the formation of supportive alliances to obtain high-value resources (van Schaik 1989). Abundant high-value anthropogenic food availability has been shown to increase group formation in bushbabies (Scheun et al. 2015, 2019); however, further research would be necessary to look at the relationship between alliance support and human food consumption to support this hypothesis.

Overall, group metrics showed that greater human food consumption was related to increased group cohesion, supporting previous work by Hockings et al. (2012) that found chimpanzee (*Pan troglodytes verus*) groups became more cohesive during crop foraging. However, more recent research on chacma baboons (*Papio ursinus*) (Bracken et al. 2022) and macaque spp. (Marty et al. 2019; Morrow et al. 2019) have shown that peri-urban primate groups are less cohesive. These group metric results support the idea that group-living animals modify the nature of their social relationships to increase their competitive power over desirable food resources (Sterck et al. 1997). These findings develop our knowledge of the flexibility in the social structure of vervet monkeys in an urban setting. However, it is important to note that the effect sizes are small and that further research is needed to confirm these findings. Future studies investigating how such increased social cohesion relates to the spatial distribution of the group around human food sources can also be useful in informing urban management strategies.

Individual level predictions

For our individual level prediction **2a**, the interaction between positive human incidents and rank significantly negatively affected the grooming indegree of vervet monkeys. Interestingly, positive human incidents reduced the effect of rank on grooming such that the grooming indegree of lower-ranking individuals increased to a comparable level with high-ranking individuals. There was no such effect on grooming outdegree, indicating that lower-ranking individuals became more attractive to groom, but themselves did not groom more partners. This result does not meet our expected directionality of individual-level prediction **2a** of within-group competition; instead, results for grooming centrality suggest a more egalitarian relationship (Sterck et al. 1997). It could be argued that this increase in social value was because of potential coalitionary support and may have represented a social exchange (Schino and Nazionale 2007); however, we do not have the data to fulfil this statement within the realms of this study, but this provides an interesting note for further research.

Our aggression metrics did meet our individual-level prediction **2a**. We found an interaction between positive human incidents and rank for aggressive eigenvector centrality, showing that the aggressive connections of higher-ranking vervet monkeys increased with a higher rate of positive human incidents. The same was true of aggression outdegree; higher rates of positive human incidents were related to an increased number of partners to whom high-ranking individuals gave aggression. These findings supported our individual-level prediction **2a** based on socioecological theory that high-value resources (positive human incidents) increase despotism and the resource-holding potential of high-ranking individuals' within the group (Isbell 1991a, b; Sterck et al. 1997; Marty et al. 2019). Furthermore, these results emphasise the importance of high-value resources to high-ranked urban vervet monkeys, highlighting the cost and benefits of these resources to the urban monkey, which is fundamental for management considerations.

Our individual-level prediction **2b** was met. We found that females were more central in their grooming networks in vervet monkeys, having a higher centrality for all three individual metrics than males. This supports the idea of female centrality in a female philopatric species (Seyfarth and Cheney 1984; Canteloup et al. 2021). This also supports previous social network studies that have shown females are more central within their networks than males (Henzi et al. 2013; Josephs et al. 2016; Borgeaud et al. 2017; Young et al. 2017)

and more recently in lion-tailed macaques (*Macaca silenus*) in the anthropogenic landscapes (Dhawale and Sinha 2022). Furthermore, the idea of female centrality endorses socioecological literature, suggesting females form coalitions under WGC (Isbell 1991a, b; Isbell and Young 2002; Sterck et al. 1997). However, it would be pertinent to explore individual rank further in future studies, notably if a males position and centrality changes within the mating period.

We found an unexpected yet consistent trend of negative human incidents across aggression and grooming metrics at the individual level. Negative human incidents positively influenced all aggressive measures. It is possible that increased aggression, both outdegree and indegree, between individuals was a result of redirected human aggression. Redirected aggression between primates is a relatively common behaviour where the individual that received aggression is more likely to be aggressive to its conspecifics (Cheney and Seyfarth 1989). Furthermore, we found that grooming eigenvector centrality increased, yet both grooming indegree and outdegree decreased, with a higher rate of negative human incidents. Previous primate literature has shown that grooming alleviates stress and anxiety (e.g. Wittig et al. 2008). If human-monkey conflict increased stress and anxiety in vervet monkeys, we would expect to see all grooming centrality measures positively increased. Nevertheless, previous literature has shown that under crowded conditions, female primates reduce their number of grooming partners; however, they maintain more selective grooming partners for future conflict avoidance (De Waal 1987; Koyama and Dunbar 1996; Judge and de Waal 1997; Judge et al. 2006). This literature focuses on captive primates under periods of short-term stress; however, their results could be applied to suggest that vervet monkeys in this study do maintain grooming rates (increased eigenvector centrality) but decrease grooming partners (decreased outdegree and indegree) under periods of short-term stress such as human-primate conflict. Furthermore, these results also support the social buffering hypothesis suggesting that under period of stress individuals may choose to groom select close associates (Wittig et al. 2008; Young et al. 2014). Overall, these results highlight the complex costs and benefits of the urban landscape (Thatcher et al. 2023), that the benefits of consuming human-derived foods override the costs of human-directed and within-group aggression.

This study presents findings from a six-month period, and the effect sizes are relatively small. Further long-term research is required to corroborate these findings and establish whether the trends reported are robust.

Conclusions

Overall, our group-level predictions were met. Group metrics assessed in this study followed socioecological predictions, suggesting increased access to anthropogenic food for vervet monkeys increases WGC. Our individual vervet monkey predictions were not so clearly met; nevertheless, this study reiterates the need for further research into the social flexibility of wildlife to anthropogenic pressures. We suggest that further research should focus on how increased social cohesion influences the spatial distribution of the group and on the direct consequences of raiding events, particularly coalition support. Furthermore, it was not possible in this study to examine the effects of intergroup encounters and competition as they were seldom witnessed because of field limitations and logistics. Nevertheless, it is likely that increasing encroachment of human populations and changes to landscape caused by urbanisation (McKinney 2006; Chakraborty et al. 2023) will affect inter-group encounters and would make an interesting topic for further research.

Considering the recent surge in ethnoprimatology and the acknowledgement of its concern for primate welfare and biodiversity (McLennan et al. 2017), we provide an important foundation for future research. We provide an assessment of five troops of vervet monkeys living in a highly anthropogenic mosaic landscape, of which they show social flexibility to adapt and thrive under these pressures. Our results largely comply with expected socioecological predictions, showing that groups from connected dominant structured groupings when are reliant upon clumped high-value anthropogenic resources. These results have important implications for urban wildlife management. Our findings demonstrate the social flexibility of urban vervet monkeys and the ways in which they dominate and exploit beneficial anthropogenic resources, highlighting the need for better public education and controlled refuse management.

Author contributions Harriet Thatcher: Conceptualisation, Methodology, Formal Analysis, Writing Original Draft; Colleen Downs: Supervision, Writing Original Draft, Funding acquisition, Resources; Nicola Koyama: Conceptualisation, Supervision, Methodology, Writing Original Draft.

Declarations

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