Journal of Urban Ecology

Journal of Urban Ecology, 2021, Vol. 7, No. (1), 1–9

doi: 10.1093/jue/juab031
Research Article

The costs of urban living: human–wildlife interactions increase parasite risk and self-directed behaviour in urban vervet monkeys

Harriet R. Thatcher ,[1,*] Colleen T. Downs[2] and Nicola F. Koyama[3]

[1]Department of Biomedical Sciences, University of Edinburgh, Teviot Place, Edinburgh, EH8 9AG, UK, [2]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01, Scottsville, Pietermaritzburg, KwaZulu-Natal 3209, South Africa and [3]Research Centre in Evolutionary Anthropology & Palaeoecology, School of Biological and Environmental Sciences, Liverpool John Moores University, Byrom Street, Liverpool, L3 3AF, UK

*Corresponding author. E-mail: harriet.thatcher@ed.ac.uk

Submitted: 19 April 2021; **Received (in revised form):** 6 September 2021. **Accepted:** 9 September 2021

Abstract

The urban landscape is a complex mosaic of costs and benefits for urban wildlife. Although many species may adapt and thrive in the urban mosaic, the complexity of this landscape can be stressful and have health implications for urban wildlife, raising concerns for zoonosis and biodiversity. In this study, we assessed how human–primate interactions influenced parasite risk and anxiety-related behaviour of urban vervet monkeys in KwaZulu-Natal, South Africa. Over 1 year, we collected and analysed faecal samples, assessing eggs per gram, species richness, and Shannon's diversity index. In addition, using behavioural sampling, we recorded self-directed scratching behaviour, as an indicator of anxiety, and human–primate interactions, both positive (human-food consumption) and negative (human–monkey aggression). To assess parasite risk in the urban mosaic, we ran three models with our parasite measures as dependent variables. Results showed that negative human interactions significantly increased with eggs per gram, species richness, and Shannon's diversity index and positive human interactions increased with both eggs per gram and species richness. Furthermore, eggs per gram significantly increased with higher scratching rate. We also tested the relationship between scratching and human interactions, finding that scratching significantly increased under higher rates of negative human incidents. Overall, results suggest that there are costs to urban living that increase anxiety-related behaviour and parasite risk despite increased food availability. Our findings are important for developing effective management strategies that focus on cohabitation rather than conflict, for the benefit of human and wildlife health.

Key words: self-directed behaviour, human–wildlife coexistence, anthropogenic, management, welfare

Introduction

Human population growth is resulting in continuous expansion and development of the urban mosaic; this expansion is consequently causing increased interactions between humans and wildlife (Soulsbury and White 2015). These interactions have multiple facets, both from the perspective of humans and wildlife (Nyhus 2016). For example, wildlife may benefit from increased access to human resources at the potential cost of human aggression (Thatcher, Downs, and Koyama 2019a,b), whereas humans may suffer losses of domestic animals and food (Dickman 2010). For both parties, the increased proximity in the urban mosaic amplifies opportunities for zoonotic transmission (Singh and Gajadhar 2014), and therefore, studies on parasite diversity are important for human–wildlife health and well-being (Díaz et al. 2006); this is of particular concern for non-human primates (hereafter known as primates) (Cooper et al. 2012).

The urban mosaic forms a complex fragmented habitat resulting in increased proximity and interactions between humans and wildlife, which are commonly linked to increased intensity and diversity of parasites in primates (Nunn, Altizer, and Altizer 2006). This trend for increased parasitism has been shown in urban primates, including Barbary macaques (*Macaca sylvanus*) (Borg et al. 2014), white-footed tamarins (*Saguinus leucopus*) (Soto-Calderón et al. 2016) and vervet monkeys (*Chlorocebus pygerythrus*) (Thatcher, Downs, and Koyama 2018). However, the effects of urbanization on primate parasite load are not consistent, and some studies have found that a more anthropogenic environment can lead to a reduction in the intensity and diversity of parasites [e.g. Balinese long-tailed macaque, *Macaca fascicularis* (Lane et al. 2011)]. A recent review on urban mammalian parasite prevalence suggests two responses, either an urban burden hypothesis that parasite susceptibility increases because of increased stresses and proximity or an urban refuge hypothesis, in that parasite levels decrease because of increased resources (Werner and Nunn 2020). Generally, findings of parasite load in anthropogenic primates are mixed, likely because of the wealth of factors that can influence parasite load (Mackenstedt, Jenkins, and Romig 2015; Cable et al. 2017); nevertheless, this does suggest that understanding interactions in the urban mosaic is important for primate health.

Wildlife living in the urban mosaic are often subject to an array of stresses that can impact an animals' biology (Kaisin et al. 2021), forcing them to adapt behavioural strategies to mitigate this stress (Ditchkoff, Saalfeld, and Gibson 2006). Previous studies have shown that increased stress in urban wildlife can result in immunosuppression, increasing parasite load (Padgett and Glaser 2003), particularly under increased anthropogenic pressures (Klaus et al. 2018). A recent review found no relationship between urbanization and stress levels across taxa; however, the authors suggest that this could be because of similar stress levels in urban and wild populations, albeit new stressors (Murray et al. 2019), or this could be interpreted as a sign of chronic stress [e.g. urban ornate tree lizards, *Urosaurus ornatus* (French, Fokidis, and Moore 2008)]. This review was conducted across wildlife taxa, suggesting that research into species-specific reactions to urban stressors was necessary (Murray et al. 2019). Furthermore, it should be considered that although the urban mosaic can have many stresses, these can be offset by the benefits of the urban landscape (e.g. human food), creating a complex attraction–avoidance balance (Thatcher, Downs, and Koyama 2019a,b).

Although research is now taking a proactive stance to focus on coexistence rather than conflict, understanding anthropogenic drivers, both positive and negative, is important for wildlife management (Thatcher, Downs, and Koyama 2020). These impacts of urban living are shown in both behavioural and physiological indicators (Nyhus 2016; Thatcher 2019). Self-directed behaviour is commonly used in primate studies as a measure of stress (Troisi and Schino 1987; Castles, Whiten, and Aureli 1999) and has been linked to environmental conditions (Troisi and Schino 1987; Ventura et al. 2005). For example, tourist pressure has been shown to increase self-directed behaviour in Barbary macaques (Maréchal et al. 2011) and spider monkeys (*Ateles geoffroyi*) (Pérez-Galicia et al. 2017). Additionally, a recent study on chacma baboons (*Papio ursinus*) showed that more anthropogenic habitats were associated with increased conflict and higher glucocorticoids, but found self-directed behaviour was greater in national parks than suburbs (Chowdhury, Brown, and Swedell 2020). Furthermore, recent research by Duboscq et al. (2016) considered multiple hypotheses to explain self-directed behaviour in female Japanese macaques (*Macaca fuscata fuscata*) including parasitological, environmental, and social. Their findings suggest that scratching is an immune response to parasites; however, still suggest that all factors should be considered within parasite analysis (Duboscq et al. 2016). These studies therefore highlight the potential use of scratching to assess stressors in the anthropogenic landscape.

Wildlife often prospers within the urban mosaic because of increased resources, particularly foraging opportunities (Lowry, Lill, and Wong 2013). Studies of urban primates show that populations can have increased body mass that can be associated with both decreased (Soto-Calderón et al. 2016) and increased (Borg et al. 2014) parasite prevalence. Additionally, a reduction in food availability has been shown to reduce immune defences (Houston et al. 2007) and hence susceptibility to disease (Murray, Keith, and Cary 1998; Eberhardt et al. 2013). Furthermore, the nutritional value of food can influence parasitism (Agostini et al. 2017), for example, human-derived food containing greater starch has been suggested to increase parasite load (Weyher, Ross, and Semple 2006; Becker, Streicker, and Altizer 2015). The nature of the urban mosaic and foraging opportunities also increases opportunities for transmission between individuals because of increased proximity (Thiel et al. 2005; Wright and Gompper 2005; Giraudeau et al. 2014). Considering that urban primates foraging is adaptive, opportunistically benefiting from urban resources (Thatcher, Downs, and Koyama 2019b, 2020), it is likely that their adaptive foraging also influences parasite risk. Understanding the multiple facets of food, nutrition, health and human–wildlife coexistence in the urban mosaic is important to predict disease transmission and support wildlife management (Chapman, Gillespie, and Goldberg 2005; Beldomenico and Begon 2010).

Vervet monkeys express a high degree of behavioural flexibility to the urban landscape, behaviourally adapting to both the positive and negative aspects of the urban mosaic (Thatcher, Downs, and Koyama 2019a,b, 2020), therefore, increasing opportunities for zoonotic transmission from wildlife to humans (Hegglin, Bontadina, and Deplazes 2015). Studies have previously considered parasitism in anthropogenic vervet monkeys (Gaetano et al. 2014; Valenta et al. 2017; Thatcher, Downs, and Koyama 2018), but have not thoroughly considered the role of human–wildlife interactions on the potential for zoonosis in the urban mosaic. Therefore, this study aims to assess how human–primate interactions in the urban mosaic influence vervet monkey parasite risk. We predicted that increased human–monkey aggression would increase parasite load, and this would correspond with an increase in anxiety indicated by self-directed scratching behaviour. We also predicted that increased access to human food would increase parasite load. Furthermore, we aimed to assess if there was a relationship between self-directed scratching behaviour and human–primate interactions. We predicted that human–monkey aggression would be stressful for vervet monkeys and therefore increase scratching rate.

Methods

Our study was conducted in Simbithi Eco-Estate, a private gated housing estate in Durban north coast, KwaZulu-Natal, South

Africa (29.5140° S, 31.2197° E). The estate forms a complex urban mosaic including a variety of housing options, leisure developments, green spaces for recreational activity as well as green-fringes of natural vegetation. The anthropogenic topography of this estate was mixed; however, there were comparable facilities throughout the estate and all were heavily managed.

Simbithi Eco-Estate has seven vervet monkey groups (Simbithi Eco-Estate 2017, pers. comm.), although this study only considered the five groups that regularly stayed within the borders of the estate. Group size varied from 14 to 42 individuals [Ballito (14): 3 males, 6 females, 5 juveniles; Farmyard (23): 4 males, 10 females, 9 juveniles; Savannah (25): 4 males, 10 female, 11 juveniles; Goodies (29): 5 males, 10 females, 14 juveniles; Herron (42): 5 males, 14 females, 23 juveniles]. All adult monkeys were identifiable via size differentiation and distinct markings. As this was the first study on these groups, their history was unknown.

Field data were collected between March 2016 and February 2017, and additional laboratory work was conducted between March 2016 and April 2017. This study's ethical approval was obtained from Liverpool John Moores University (NK_HT/2017-6).

Faecal sample collection and parasite identification methods

We collected faecal samples opportunistically during daily follows, immediately after defecation. Using latex gloves, we took a sample of faeces from the centre of the stool (not including any outer elements, e.g. vegetation/soil, to avoid contamination by free-living nematodes in the immediate environment). We then homogenized the sample by hand using wooden spatula and a sterile tube to make sure that there was an even representation of the centre of the faecal matter. The homogenized sample was stored in a sterile tube pre-prepared with 70% ethanol and was labelled with the date, time, species, age class (adult/juvenile) and sex (or monkey ID if known), group name and geographic location measured with a global positioning system (Garmin Etrex 10). We then shook the tubes vigorously to maximize contact between the sample and ethanol.

All samples were stored in ambient conditions and tested in laboratory conditions, within ~4 weeks of collection. For parasite analyses, we adapted the standard faecal flotation protocol (Gillespie 2006). We used a pipette to take a sample of the prepared specimen from the centre of the tube and used this sample to fill both chambers of a McMaster slide. We scanned a two-chamber McMaster slide containing the centrifuged sample using the Å~10 objective lens of a compound microscope. We identified and counted the presence of any parasite eggs, larvae, and cysts. We then scanned the slide under Å~40 objective lens to confirm the presence or absence of protozoan cysts. For all analysis, we only counted any elements seen within the two McMaster chamber squares identifying samples to genus level.

Behavioural methods

We conducted behavioural observations from dawn till dusk, following one group per day. The day was split into three time periods (morning, midday, afternoon) to collect a minimum of one observation per time slot per monkey per month for a 1-year period (March 2016–February 2017); 20 min focal animal observations (Altmann 1974) were conducted for all adults within each of the five groups. We collected data using the Prim8 behavioural software (McDonald and Johnson 2014) on a handheld Lenovo tablet. During focal observations, we recorded all instances of self-directed behaviour, including self-scratch, self-groom, and self-touch behaviours (Schino et al. 1988; Castles, Whiten, and Aureli 1999). We calculated the number of bouts performed per focal observation and converted this to a frequency as in previous studies (Castles, Whiten, and Aureli 1999; Sclafani et al. 2012). For comparison to our human interactions variables, we converted this to a rate per hour.

Human–wildlife interactions

During daily follows, we used all occurrence sampling to record all interactions between humans and vervet monkeys. We identified a human-related incident as any occasion when at least one vervet monkey interacted with humans or their possessions (car, house, bin, etc.). For positive human interactions, we included any form of anthropogenic food consumption (e.g. bread, fruit, pizza). An incident was classed as terminated once all anthropogenic food was consumed. If the monkeys then obtained anthropogenic food after 20 min, we classed this as a new event. Negative human interactions were classed as any form of human aggression directed towards vervet monkeys (chase, rocks thrown, etc.). Such interactions represent a cost to the vervet monkey because of the energy expended (running away) and the risk of injury. We classed an incident as terminated once all parties had retreated, and we recorded new events if there had been no incident in the prior 20 min. Positive and negative human interactions were not mutually exclusive; a human event could be coded twice as both positive and negative [e.g. monkey takes food from a human's house (positive) and is chased away (negative)]. For human interaction values, we calculated a monthly rate (per hour) per group based on how many interactions were observed according to hours of field observation each month.

Statistical analyses

We obtained 673 faecal samples. An average of 5.62 (± 0.48 SD) samples was collected per individual over the year-long study and no individual was sampled more than once a month (Supplementary Table S1). For 390 of the samples, monkey identification was recorded, for the remaining 283, only the group and sex were identifiable. We, therefore, combined all parasite recordings per group to create a group monthly average. We converted raw data from the McMaster analysis to eggs per gram (Dunn and Keymer 1986), we counted the number of species present as a measure of parasite richness per sample and further calculated Shannon's diversity index as a measure of species relative abundance and evenness. We converted this information into a group monthly average. All our dependent and independent variables were analysed as an average group monthly value to allow more comparison within our study and the wider literature.

All data were analysed using R statistical software, and the significance level was set at $P \leq 0.05$. To assess our aims, we ran two separate mixed model structures using the lme4 package (Bates 2010). We calculated the variation inflation index of each predictor for inclusion in our models using the CAR package (Fox et al. 2007), setting the inclusion level at <3 (Zuur et al. 2010). We assessed the fit of each model by graphically checking residuals for normal distribution and that the assumptions of our model were not violated.

We tested the distribution of all dependent variables using Shapiro–Wilk's test and graphical visualization (Ghasemi and

Zahediasl 2012). For our first model assessing parasite risk, both species richness and eggs per gram were found to be normally distributed, we, therefore, ran two linear mixed models with parasite eggs per gram and parasite species richness as the dependent variable. Shannon's diversity index was not normally distributed; therefore, for this dependent variable, we ran a generalized linear mixed model for non-parametric data with a gamma error distribution using a log link function. We created *a priori* maximum models that included positive human interactions, negative human interactions, self-directed behaviour, and group size as fixed effects. Furthermore, we ran an interaction between negative human interactions and scratching. We also included group identification as a random effect. We did not include season as a fixed effect due to model overfitting but mean values can be seen in the supplementary material (Supplementary Table S2).

To assess our second aim on anxiety, we found self-directed behaviour was not normally distributed using a Shapiro–Wilk's test and graphical visualization (Ghasemi and Zahediasl 2012). We, therefore, ran a generalized linear mixed model for non-parametric data with a gamma error distribution using a log link function. We created an *a priori* maximum model with self-directed behaviour as the dependent variable. We included positive human interactions, negative human interactions, and group size as fixed effects, as well as including group identification as a random effect.

Results

Parasites identified were *Coccidia* spp., *Strongyloides* spp., *Tricuris* spp., *Ascaris* spp., and *Oesophagostomum* spp. and these were found in the faeces of all five vervet monkey groups (supplementary Table S3).

From our first model assessing parasite risk, we found that eggs per gram significantly increased with negative human interactions ($P = 0.001$, Table 1, Fig. 1a), positive human interactions ($P = 0.008$, Table 1, Fig. 1b) and self-directed behaviour ($P = 0.001$, Table 1, Fig. 1c). We found that species richness increased significantly with negative human interactions ($P = 0.008$, Table 2, Fig. 2a) and positive human interactions ($P = 0.002$, Table 2, Fig. 2b). Furthermore, we found that Shannon's diversity index significantly increased with negative human interactions ($P = 0.017$, Table 3, Fig. 3).

Our second model assessing anxiety showed that self-directed scratching behaviour significantly increased with a greater rate of negative human interactions ($P = 0.008$, Table 4, Fig. 4).

Discussion

We found that both vervet monkey species richness, eggs per gram, and Shannon's diversity index were influenced by human interactions. In addition, eggs per gram positively increased with higher rates of scratching. What is more, our second model showed that self-directed scratching behaviour significantly increased with a higher rate of negative human interactions. Our main results, therefore, supported our predictions and raise important points for urban primate welfare and zoonotic transmission.

The significant positive trend for both positive and negative human interactions on vervet monkeys' parasite species richness and eggs per gram, and negative human interactions on Shannon's diversity index, supports previous research that anthropogenic landscapes increase parasite load (Borg et al. 2014; Soto-Calderón et al. 2016; Thatcher, Downs, and Koyama 2018). This could be because of increased transmission at clumped resources of high-value food, resulting in more frequent interactions and increased proximity to conspecifics increasing exposure to parasites (Nunn et al. 2003; Gompper and Wright 2005; Nunn, Altizer, and Altizer 2006; Kamiya et al. 2014; Galbraith et al. 2017). Artificial food patches have previously been suggested as a management technique for urban primates to provide an alternate regular food supply whilst reducing interactions between primates and humans (Kaplan et al. 2011). However, our findings would dispute this suggestion as this may further increase grouping and transmission rates. Instead, management should consider reducing anthropogenic foraging opportunities to reduce interactions between humans and primates (both positive and negative) and ensure more dispersed alternate foraging resources are available.

Increased parasite burden under negative human interactions could again support a proximity hypothesis (Nunn et al. 2003; Gompper and Wright 2005; Nunn, Altizer, and Altizer 2006; Kamiya et al. 2014; Galbraith et al. 2017), or this could be a response to human aggression (Chowdhury, Brown, and Swedell 2020). These results raise concerns from an urban wildlife welfare perspective, suggesting that increased human conflict and negative human interactions can have potential health repercussions. Therefore, these results should actively be applied to encourage cohabitation between humans and wildlife. Furthermore, research into the multiple facets of human–wildlife interactions is needed to develop our understanding of the drivers behind these negative interactions, both from a human and primate perspective to reduce conflict and improve urban wildlife welfare.

Our results also showed that greater positive human interactions increased both parasite eggs per gram and species

Table 1: Linear mixed model results of the fixed effects on eggs per gram of urban vervet monkeys, Simbithi Eco-estate, KwaZulu-Natal, South Africa.

					Confidence intervals	
	Estimate	Standard error	Degrees of freedom	P values	Lower	Upper
Intercept	3.72	1.55	3.77	0.001	0.81	6.78
Negative human interactions	**3.90**	**0.94**	**52.58**	**0.001**	**2.13**	**5.69**
Scratching	**0.49**	**0.12**	**50.83**	**0.001**	**0.27**	**0.71**
Positive human interactions	**2.90**	**1.05**	**49.21**	**0.008**	**0.90**	**4.87**
Group size	–0.10	0.05	3.17	0.150	–0.20	0.00
Negative human interactions × scratching	–0.17	0.11	53.66	0.136	–0.38	0.04

Bold results indicate a significant effect.

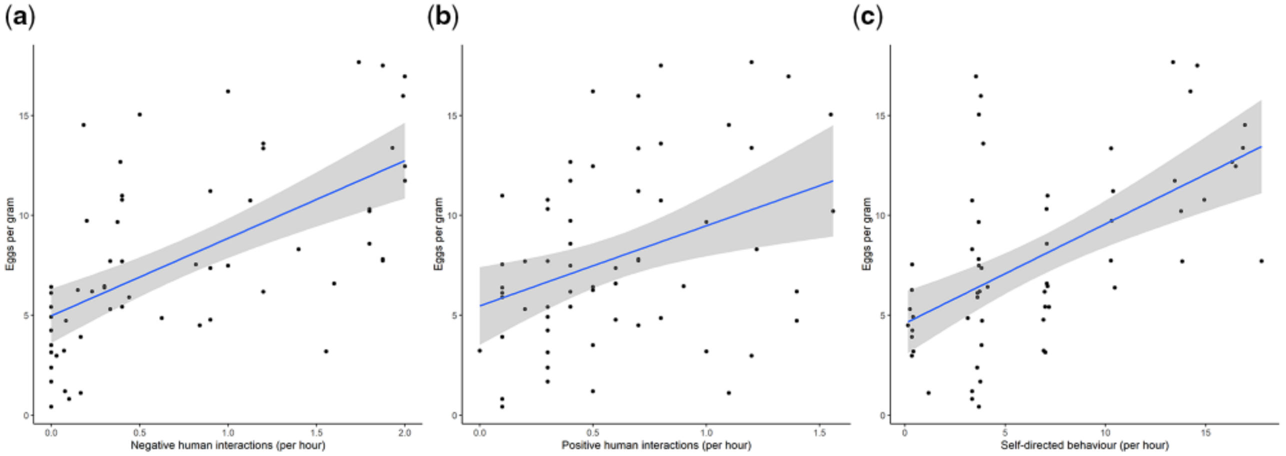

Figure 1: Parasite eggs per gram obtained from vervet monkey faecal samples at Simbithi Eco-Estate, KwaZulu-Natal, South Africa, in the present study, where (a) shows the significant positive effect of negative human interactions on parasite eggs per gram, (b) shows the significant positive effect of positive human interactions on parasite eggs per gram and (c) shows the significant positive effect of self-directed behaviour. Grey areas represent 95% confidence intervals

Table 2: Linear mixed model results of the fixed effects on species richness of urban vervet monkeys at Simbithi Eco-estate, KwaZulu-Natal, South Africa in the present study.

					Confidence intervals	
	Estimate	Standard error	Degrees of freedom	*P* values	Lower	Upper
Intercept	1.49	0.08	4.61	0.118	0.09	2.90
Negative human interactions	**0.63**	**0.02**	**52.44**	**0.008**	**0.22**	**1.12**
Scratching	0.03	0.03	52.48	0.309	−0.02	0.08
Positive human interactions	**0.82**	**0.03**	**50.17**	**0.002**	**0.36**	**1.34**
Group size	−0.01	0.03	4.52	0.843	−0.05	0.04
Negative human interactions × scratching	0.04	0.03	52.08	0.849	−0.050.05	

Bold results indicate a significant effect.

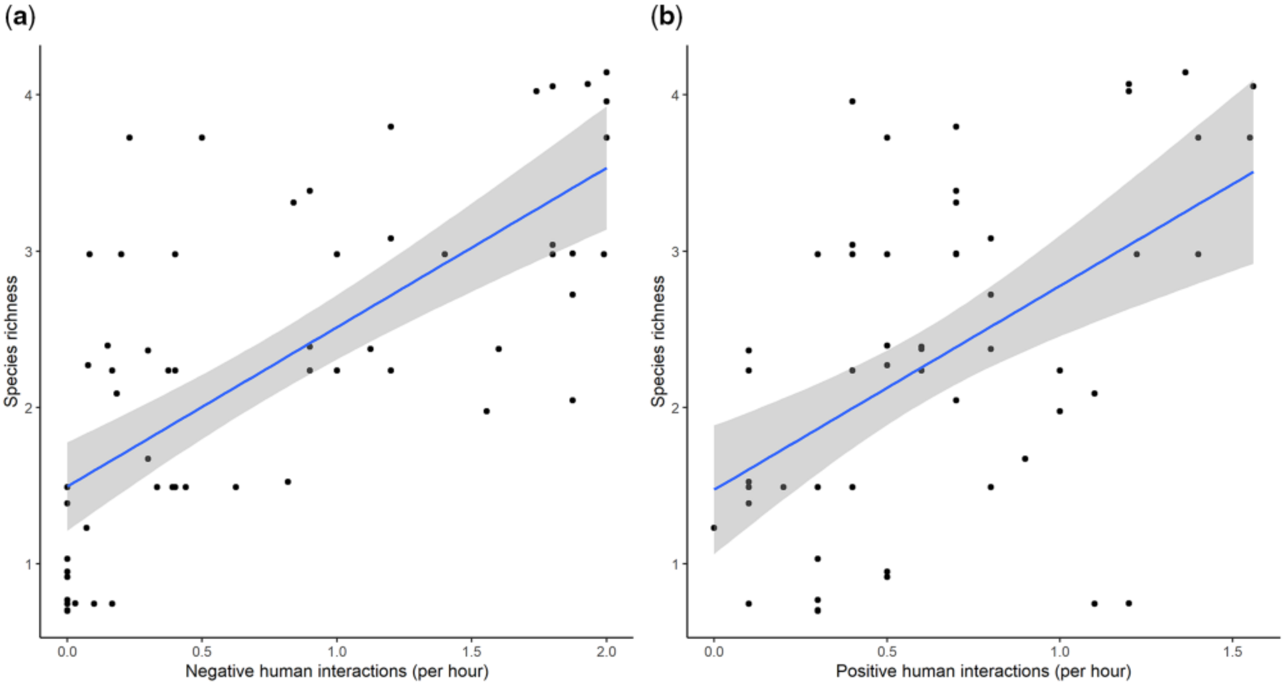

Figure 2: Parasite richness obtained from vervet monkey faecal samples at Simbithi Eco-Estate, KwaZulu-Natal, South Africa, in the present study, where (a) shows the significant positive effect of negative human interactions and (b) shows the significant positive effect of positive human interactions. Grey areas represent 95% confidence intervals

Table 3: Table 3 Generalised linear mixed model results of the fixed effects on Shannon's diversity index of urban vervet monkeys at Simbithi Eco-estate, KwaZulu-Natal, South Africa in the present study. Residual degrees of freedom= 54.

				Confidence intervals	
	Estimate	Standard error	P values	Lower	Upper
Intercept	2.31	0.09	<0.001	9.93	10.28
Negative human interactions	**0.14**	**0.06**	**0.017**	**0.03**	**0.26**
Scratching	0.01	0.01	0.071	–0.00	0.03
Positive human interactions	0.09	0.06	0.119	0.03	0.21
Group size	–0.01	0.00	0.148	–0.00	0.02
Negative human interactions × Scratching	–0.01	0.01	0.255	–0.02	0.05

Bold results indicate a significant effect.

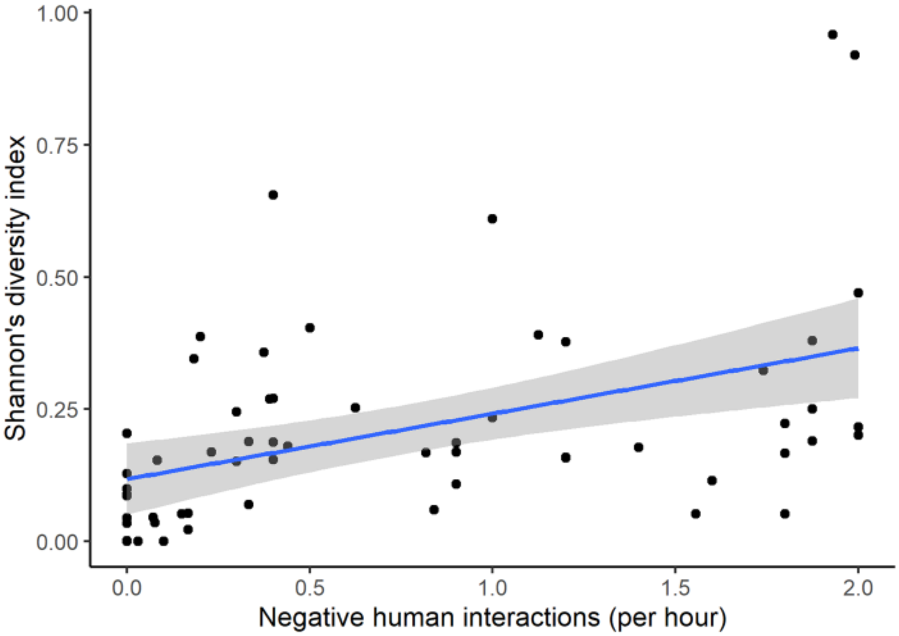

Figure 3: The positive significant effect of negative human interactions on Shannon's diversity index of urban, vervet monkeys at Simbithi Eco-Estate, KwaZulu-Natal, South Africa in the present study. Grey areas represent 95% confidence intervals

Table 4: Table 4 Generalised linear mixed model results of the fixed effects on self-directed scratching behaviour of urban vervet monkeys at Simbithi Eco-estate, KwaZulu-Natal, South Africa, in the present study. Residual degrees of freedom= 54.

				Confidence intervals	
	Estimate	Standard error	P values	Lower	Upper
Intercept	2.90	0.15	<0.001	0.79	4.47
Negative human interactions	**0.14**	**0.55**	**0.008**	**0.96**	**1.05**
Positive human interactions	–0.11	0.10	0.906	–1.45	1.55
Group size	–0.01	0.01	0.165	–0.07	8.33

Bold results indicate a significant effect.

richness. Positive aspects of the anthropogenic mosaic, such as increased human food, have previously been shown to increase parasite load because of high starch and poor nutrition (Weyher, Ross, and Semple 2006; Becker, Streicker, and Altizer 2015). Opposing research has shown that anthropogenic food can reduce foraging effort and hence parasite risk, e.g. through decreased ranging requirements (Nunn and Dokey 2006) and increased immune response (Ezenwa 2004). Nevertheless, research on this study population has shown that anthropogenic landscape characteristics can decrease daily movement but increase ranging (Thatcher, Downs, and Koyama 2019a,b) and suggest a high degree of foraging flexibility (Thatcher, Downs,

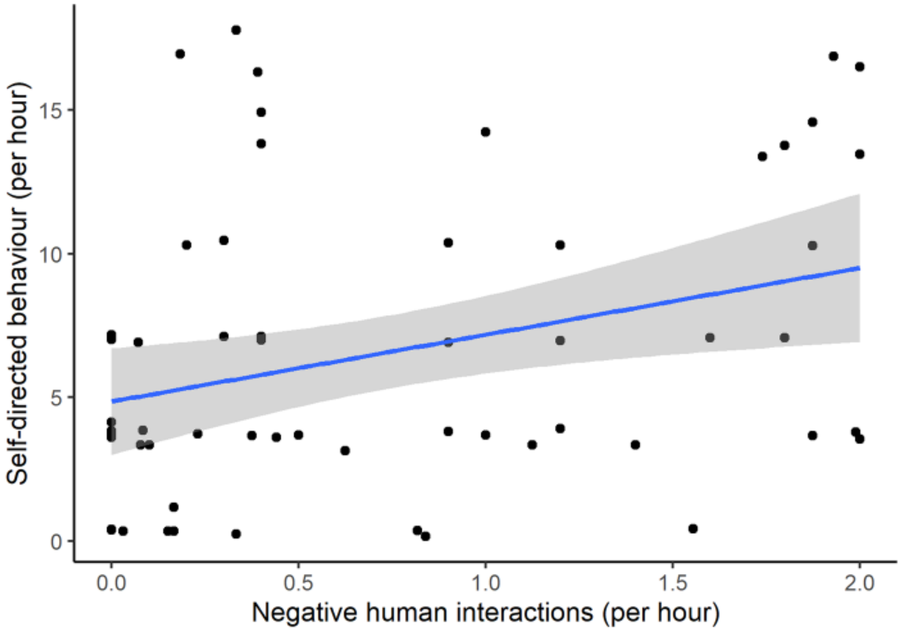

Figure 4: The positive significant effect of negative human interactions on the self-directed behaviour of urban vervet monkeys at Simbithi Eco-Estate, KwaZulu-Natal, South Africa in the present study. Grey areas represent 95% confidence intervals

and Koyama 2020), potentially supporting this positive trend in results. In addition, previous research on this population has shown that positive human interactions increase the grooming rate but decrease the foraging rate (Thatcher, Downs, and Koyama 2019b), suggesting that increased foraging on human food may increase time available for socializing and grooming and hence parasite transmission. However, these studies also show the complexity of positive and negative human interactions within the urban landscape, that one factor cannot be considered independently and that the urban mosaic creates a complex scale of interactions for urban wildlife.

Self-directed behaviour significantly increased with parasite eggs per gram. This supported our prediction that parasite load may be influenced by anxiety (Hart 1990; Giraudeau et al. 2014) but could also suggest that increased self-directed behaviour relative to parasite load may be a behavioural response to parasite burden (Duboscq et al. 2016). Although our interactions between negative human interactions and self-directed behaviour were not significant, as the two factors independently increased parasite risk, it does suggests a cost to urban living and supports previous research showing the links between stress, parasitism, and the urban mosaic [e.g. house finches, *Haemorhous mexicanus* (Giraudeau et al. 2014)]. More so, our second model showed that scratching frequency significantly increased with a greater rate of negative human interactions. This result, therefore, supports the notion that anxiety levels increase in the urban mosaic (Maréchal et al. 2011; Pérez-Galicia et al. 2017), suggesting that human aggression is costly to vervet monkeys with potential health effects.

Our study's results and the interactions between humans and primates may have repercussions for management from a zoonotic perspective. Contact with humans and human property may expose animals to zoonotic diseases (Satterthwaite 2003; Seto et al. 2013). Therefore, the increased presence and interaction with humans is likely to increase the risk of zoonotic disease transmission for this study population. More so, it is possible that the location and nature of this field-site will increase opportunities for both reverse zoonosis and zoonotic transmissions, due to the close proximity to highly urbanized developments and a high degree of landscape change (Brearley et al. 2013), as well as proximity to other wildlife, both domestic (e.g. dogs) and wild (e.g. duiker, *Bovidae*, and Cape porcupine, *Hystrix africaeaustralis*) (Daszak, Cunningham, and Hyatt 2001). Although we cannot make any direct recommendations on zoonotic risks or fitness implications of the parasites found in this study as we have only identified species to genus level, our results suggest that vervet monkeys are in increased contact with humans interacting through opportunistic foraging, direct provisioning and human-directed aggression. The results of this study do provide a further level of detail to the ongoing complexity of anthropogenic disease ecology (Brearley et al. 2013; Mackenstedt, Jenkins, and Romig 2015); however, future studies should be conducted to investigate the multiple facets of the anthropogenic environment from a zoonotic perspective on a broader scale for the benefit of both humans and wildlife.

Conclusions

The results of this study highlight human interactions increase parasite risk. Furthermore, our results highlight the potential costs of these interactions. Generally, the information presented here raises concerns for urban wildlife both from a welfare perspective, increasing anxiety, and also a biological health perspective, increasing parasite risk. Nevertheless, it should be noted that this study population is highly adaptable to the urban landscape, and the population is continuing to thrive (Thatcher 2019). Therefore, although results suggest a cost to urban living, these costs are likely outweighed by the benefits, creating a complex urban-mosaic landscape.

Supplementary data

Supplementary data are available at *JUECOL* online.

Acknowledgements

We would like to thank Simbithi Eco-Estate for allowing us to conduct our research within their estate and providing support through this project. We would also like to thank Liverpool John Moores University (UK), the University of KwaZulu-Natal (ZA), and the National Research Foundation (ZA, 98404) for their support during this period.

Funding

This work was supported by an Erasmus Mundus AESOP (*A European and South African Partnership on Heritage and Past*) grant (ES15DM0025) and Liverpool John Moores scholarship awarded to H.R.T.

Conflict of interest statement. None declared.

Data availability

Data are available from the corresponding author on request.

References

Agostini, I. et al. (2017) 'Experimental Testing of Reciprocal Effects of Nutrition and Parasitism in Wild Black Capuchin Monkeys', *Scientific Reports*, **7**: 12778–11.

Altmann, J. (1974) 'Observational Study of Behavior: Sampling Methods', *Behaviour*, **49**: 227–66.

Bates, D. M. (2010) *lme4: Mixed-Effects Modeling with R*. New York, NY: Springer Science+Business Media.

Becker, D. J., Streicker, D. G., and Altizer, S. (2015) 'Linking Anthropogenic Resources to Wildlife–Pathogen Dynamics: A Review and Meta-Analysis', *Ecology Letters*, **18**: 483–95.

Beldomenico, P. M., and Begon, M. (2010) 'Disease Spread, Susceptibility and Infection Intensity: Vicious Circles?', *Trends in Ecology & Evolution*, **25**: 21–7.

Borg, C. et al. (2014) 'A Comparison of Body Size, Coat Condition and Endoparasite Diversity of Wild Barbary Macaques Exposed to Different Levels of Tourism', *Anthrozoös*, **27**: 49–63.

Brearley, G. et al. (2013) 'Wildlife Disease Prevalence in Human-Modified Landscapes', *Biological Reviews of the Cambridge Philosophical Society*, **88**: 427–42.

Cable, J. et al. (2017) 'Global Change, Parasite Transmission and Disease Control: Lessons from Ecology', *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **372**: 20160088.

Castles, D. L., Whiten, A., and Aureli, F. (1999) 'Social Anxiety, Relationships and Self-Directed Behaviour Among Wild Female Olive Baboons', *Animal Behaviour*, **58**: 1207–15.

Chapman, C. A., Gillespie, T. R., and Goldberg, T. L. (2005) 'Primates and the Ecology of Their Infectious Diseases: How Will Anthropogenic Change Affect Host-Parasite Interactions?', *Evolutionary Anthropology: Issues, News, and Reviews*, **14**: 134–44.

Chowdhury, S., Brown, J., and Swedell, L. (2020) 'Anthropogenic Effects on the Physiology and Behaviour of Chacma Baboons in the Cape Peninsula of South Africa', *Conservation Physiology*, **8**: coaa066.

Cooper, N. et al. (2012) 'Phylogenetic Host Specificity and Understanding Parasite Sharing in Primates', *Ecology Letters*, **15**: 1370–7.

Daszak, P., Cunningham, A. A., and Hyatt, A. D. (2001) 'Anthropogenic Environmental Change and the Emergence of Infectious Diseases in Wildlife', *Acta Tropica*, **78**: 103–16.

Díaz, S. et al. (2006) 'Biodiversity Loss Threatens Human Well-Being', *PLoS Biology*, **4**: e277.

Dickman, A. J. (2010) 'Complexities of Conflict: The Importance of considering Social Factors for Effectively Resolving Human–Wildlife Conflict', *Animal Conservation*, **13**: 458–66.

Ditchkoff, S. S., Saalfeld, S. T., and Gibson, C. J. (2006) 'Animal Behavior in Urban Ecosystems: Modifications Due to Human-Induced Stress', *Urban Ecosystems*, **9**: 5–12.

Duboscq, J. et al. (2016) 'Scratch That Itch: Revisiting Links between Self-Directed Behaviour and Parasitological, Social and Environmental Factors in a Free-Ranging Primate', *Royal Society Open Science*, **3**: 160571.

Dunn, A., and Keymer, A. (1986) 'Factors Affecting the Reliability of the McMaster Technique', *Journal of Helminthology*, **60**: 260–2.

Eberhardt, A. T. et al. (2013) 'Parasitism and Physiological Trade-Offs in Stressed Capybaras', *PLoS One*, **8**: e70382.

Ezenwa, V. O. (2004) 'Interactions among Host Diet, Nutritional Status and Gastrointestinal Parasite Infection in Wild Bovids', *International Journal for Parasitology*, **34**: 535–42.

Fox, J. et al. (2007) 'The Car Package', *R Found Stat Comput*.

French, S. S., Fokidis, H. B., and Moore, M. C. (2008) 'Variation in Stress and Innate Immunity in the Tree Lizard (*Urosaurus ornatus*) across an Urban–Rural Gradient', *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology*, **178**: 997–1005.

Gaetano, T. J. et al. (2014) 'Mapping Correlates of Parasitism in Wild South African Vervet Monkeys (*Chlorocebus aethiops*)', *South African Journal of Wildlife Research*, **44**: 56–70.

Galbraith, J. A. et al. (2017) 'Experimental Feeding Regime Influences Urban Bird Disease Dynamics', *Journal of Avian Biology*, **48**: 700–13.

Ghasemi, A., and Zahediasl, S. (2012) 'Normality Tests for Statistical Analysis: A Guide for Non-Statisticians', *International Journal of Endocrinology and Metabolism*, **10**: 486–9.

Gillespie, T. R. (2006) 'Noninvasive Assessment of Gastrointestinal Parasite Infections in Free-Ranging Primates', *International Journal of Primatology*, **27**: 1129–43.

Giraudeau, M. et al. (2014) 'Parasites in the City: Degree of Urbanization Predicts Poxvirus and Coccidian Infections in House Finches (*Haemorhous mexicanus*)', *PLoS One*, **9**: e86747.

Gompper, M. E., and Wright, A. N. (2005) 'Altered Prevalence of Raccoon Roundworm (*Baylisascaris procyonis*) Owing to Manipulated Contact Rates of Hosts', *Journal of Zoology*, **266**: 215–9.

Hart, B. L. (1990) 'Behavioral Adaptations to Parasites and Pathogens', *Neurosci Biobehav Rev*, **14**: 94.

Hegglin, D., Bontadina, F., and Deplazes, P. (2015) 'Human-Wildlife Interactions and Zoonotic Transmission of *Echinococcus multilocularis*', *Trends in Parasitology*, **31**: 167–73.

Houston, A. I. et al. (2007) 'The Effect of Energy Reserves and Food Availability on Optimal Immune Defence', *Proceedings. Biological Sciences*, **274**: 2835–42.

Kaisin, O. et al. (2021) 'A Meta-Analysis of Anthropogenic Impacts on Physiological Stress in Wild Primates', *Conservation Biology : The Journal of the Society for Conservation Biology*, **35**: 101–14.

Kamiya, T. et al. (2014) 'What Determines Species Richness of Parasitic Organisms? A Meta-Analysis across Animal, Plant and Fungal Hosts', *Biological Reviews of the Cambridge Philosophical Society*, **89**: 123–34.

Kaplan, B. S. et al. (2011) ‘A Low-Cost Manipulation of Food Resources Reduces Spatial Overlap between Baboons (*Papio ursinus*) and Humans in Conflict’, *International Journal of Primatology*, **32**: 1397–412.

Klaus, A. et al. (2018) ‘Fecal Parasite Risk in the Endangered Proboscis Monkey is Higher in an Anthropogenically Managed Forest Environment Compared to a Riparian Rain Forest in Sabah, Borneo’, *PLoS One*, **13**: e0195584.

Lane, K. E. et al. (2011) ‘The Anthropogenic Environment Lessens the Intensity and Prevalence of Gastrointestinal Parasites in Balinese Long-Tailed Macaques (*Macaca fascicularis*)’, *Primates; Journal of Primatology*, **52**: 117–28.

Lowry, H., Lill, A., and Wong, B. (2013) ‘Behavioural Responses of Wildlife to Urban Environments’, *Biological Reviews of the Cambridge Philosophical Society*, **88**: 537–49.

Mackenstedt, U., Jenkins, D., and Romig, T. (2015) ‘The Role of Wildlife in the Transmission of Parasitic Zoonoses in Peri-Urban and Urban Areas’, *International Journal for Parasitology. Parasites and Wildlife*, **4**: 71–9.

Maréchal, L. et al. (2011) ‘Impacts of Tourism on Anxiety and Physiological Stress Levels in Wild Male Barbary Macaques’, *Biological Conservation*, **144**: 2188–93.

McDonald, M., and Johnson, S. (2014) ‘There’s an App for That’: A New Program for the Collection of Behavioural Field Data’, *Animal Behaviour*, **95**: 81–7.

Murray, D. L., Keith, L. B., and Cary, J. R. (1998) ‘Do Parasitism and Nutritional Status Interact to Affect Production in Snowshoe Hares?’, *Ecology*, **79**: 1209–22.

Murray, M. H. et al. (2019) ‘City Sicker? A Meta-Analysis of Wildlife Health and Urbanization’, *Frontiers in Ecology and the Environment*, **17**: 575–83.

Nunn, C., Altizer, S., and Altizer, S. M. (2006) *Infectious Diseases in Primates: Behavior, Ecology and Evolution*. Oxford, UK: Oxford University Press.

Nunn, C. L. et al. (2003) ‘Comparative Tests of Parasite Species Richness in Primates’, *The American Naturalist*, **162**: 597–614.

——, and Dokey, A. T.-W. (2006) ‘Ranging Patterns and Parasitism in Primates’, *Biology Letters*, **2**: 351–4.

Nyhus, P. J. (2016) ‘Human–Wildlife Conflict and Coexistence’, *Annual Review of Environment and Resources*, **41**: 143–71.

Padgett, D. A., and Glaser, R. (2003) ‘How Stress Influences the Immune Response’, *Trends in Immunology*, **24**: 444–8.

Pérez-Galicia, S. et al. (2017) ‘Visitor Effect on the Behavior of a Group of Spider Monkeys (*Ateles geoffroyi*) Maintained at an Island in Lake Catemaco, Veracruz/Mexico’, *Zoo Biology*, **36**: 360–6.

Satterthwaite, D. (2003) ‘The Links between Poverty and the Environment in Urban Areas of Africa, Asia, and Latin America’, *The Annals of the American Academy of Political and Social Science*, **590**: 73–92.

Schino, G. et al. (1988) ‘Allogrooming as a Tension-Reduction Mechanism: A Behavioral Approach’, *American Journal of Primatology*, **16**: 43–50.

Sclafani, V. et al. (2012) ‘Scratching around Mating: Factors Affecting Anxiety in Wild Lemur Catta’, *Primates; Journal of Primatology*, **53**: 247–54.

Seto, K. C. et al. (2013) ‘A Global Outlook on Urbanization’, in T. Elmqvist et al. (eds) *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities*. Dordrecht, the Netherlands: Springer. 1-12

Singh, B. B., and Gajadhar, A. A. (2014) ‘Role of India’s Wildlife in the Emergence and Re-emergence of Zoonotic Pathogens, Risk Factors and Public Health Implications’. *Acta Tropica* **138**: 67–77.

Soto-Calderón, I. D. et al. (2016) ‘Physiological and Parasitological Implications of Living in a City: The Case of the White-Footed Tamarin (*Saguinus leucopus*)’. *American Journal of Primatology*, **78**: 1272–81.

Soulsbury, C. D., and White, P. C. L. (2015) ‘Human-Wildlife Interactions in Urban Areas: A Review of Conflicts, Benefits and Opportunities’, *Wildlife Research*, **42**: 541–53.

Thatcher, H. R. (2019) ‘Anthropogenic Influences on the Behavioural Ecology of Urban Vervet Monkeys’, PhD thesis, Liverpool John Moores University, UK.

——, Downs, C. T., and Koyama, N. F. (2019a) ‘Positive and Negative Interactions with Humans Concurrently Affect Vervet Monkey (*Chlorocebus pygerythrus*) Ranging Behavior’, *International Journal of Primatology*, **40**: 496–510.

——, ——, and —— (2019b) ‘Anthropogenic Influences on the Time Budgets of Urban Vervet Monkeys’, *Landscape and Urban Planning*, **181**: 38–44.

——, ——, and —— (2020) ‘Understanding Foraging Flexibility in Urban Vervet Monkeys, *Chlorocebus pygerythrus*, for the Benefit of Human-Wildlife Coexistence’, *Urban Ecosystems*, **23**: 1349–57.

——, Downs, C. T. C. T., and Koyama, N. F. N. F. (2018) ‘Using Parasitic Load to Measure the Effect of Anthropogenic Disturbance on Vervet Monkeys’, *EcoHealth*, **15**: 676–81.

Thiel, T. et al. (2005) ‘Characterization of Canarypox-like Viruses Infecting Endemic Birds in the Galápagos Islands’, *Journal of Wildlife Diseases*, **41**: 342–53.

Troisi, A., and Schino, G. (1987) ‘Environmental and Social Influences on Autogrooming Behaviour in a Captive Group of Java Monkeys’, *Behaviour*, **100**: 292–302.

Valenta, K. et al. (2017) ‘Comparison of Gastrointestinal Parasite Communities in Vervet Monkeys’, *Integrative Zoology*, **12**: 512–20.

Ventura, R. et al. (2005) ‘Differential Effects of Ambient Temperature and Humidity on Allogrooming, Self-Grooming, and Scratching in Wild Japanese Macaques’, *American Journal of Physical Anthropology*, **126**: 453–7.

Werner, C. S., and Nunn, C. L. (2020) ‘Effect of Urban Habitat Use on Parasitism in Mammals: A Meta-Analysis’, *Proceedings. Biological Sciences*, **287**: 20200397.

Weyher, A. H., Ross, C., and Semple, S. (2006) ‘Gastrointestinal Parasites in Crop Raiding and Wild Foraging *Papio anubis* in Nigeria’, *International Journal of Primatology*, **27**: 1519–34.

Wright, A. N., and Gompper, M. E. (2005) ‘Altered Parasite Assemblages in Raccoons in Response to Manipulated Resource Availability’, *Oecologia*, **144**: 148–56.

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010) ‘A Protocol for Data Exploration to Avoid Common Statistical Problems’, *Methods in Ecology and Evolution*, **1**: 3–14.