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Anthropogenic influences on the time budgets of urban vervet monkeys

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ABSTRACT

Continuing urban developments are ecologically changing many landscapes. A greater understanding of how wildlife adapt behaviorally to these changes is necessary to inform management decisions. Time is a valuable resource to wildlife and a reflection of ecological pressures on the behavioral repertoire of an animal. Data on urban vervet monkey, *Chlorocebus pygerythrus,* time budgets are generally limited and dated. We aimed to investigate the effect of anthropogenic influences, both human food consumption (positive) and human-monkey conflict (negative) on the time budgets of vervet monkeys in an urban landscape. We collected 20 min. focal animal observations and used generalized linear mixed models to assess the variation in time budget between five urban vervet monkey groups differing in anthropogenic contact over one year. We recorded anthropogenic interactions ad lib. as positive and negative. Our results showed seasonal influences across all behaviors. Furthermore, anthropogenic disturbance influenced all aspects of time budget to some degree. We found a positive interaction effect between positive and negative human incidents on foraging, and a negative interaction effect on movement and social behavior. Overall, vervet monkeys exhibited behavioral flexibility in the urban landscape. We suggest a complex association of costs and benefits to urban living.

1. Introduction

Increased human populations and urban developments are transforming many wildlife habitats (McKinney, 2006). Human expansion has led to a growing interest in understanding behavioral responses of species to urbanization for urban management plans (e.g. Jokimäki et al., 2011). Wildlife has been shown to adapt to these changes in many ways including modifying foraging behavior, predator behaviors and activity patterns (Jokimäki et al., 2011). Information on how wildlife adapt behaviorally to these changes can be key for management decisions (Ditchkoff, Saalfeld, & Gibson, 2006; Marzluff, Bowman, & Donnelly, 2001). Time budgets have been applied to a variety of species to study the effect of varying levels anthropogenic disturbance (e.g. Jokimäki et al., 2011). However, studies including high-density towns and cities are scarce, furthermore, positive associations of urban living for wildlife behavior are rarely considered, despite being necessary, to develop suitable management plans (McLennan, Spagnoletti, & Hockings, 2017).

Understanding the relationship between an animal and its environment can provide essential information for conservation management and urban planning (Patterson, Kalle, & Downs, 2018). Time budgets provide a useful method to test ecological hypotheses (Isbell & Young, 1993) as they allow the representation of time allocation where trade-offs in behaviors are illustrative of the resources and time available (Dunbar, Korstjens & Lehmann, 2009). Time budget analyses have been employed across urban wildlife to demonstrate the effects of urbanization and landscape changes (burrowing owls, *Athene cunicularia hypugaea*: Chipman et al., 2008; gray squirrels, *Sciurus carolinensis:* Parker, Gonzales, & Nilon, 2014; bottlenose dolphins, *Tursiops aduncus*: Steiner, 2012).

Rapid human population growth and land-use changes have transformed many primate habitats (Estrada, Raboy, & Oliveira, 2012; Mckinney, 2015) and have resulted in a directional shift towards ethnoprimatology (Fuentes & Hockings, 2010; Hockings et al., 2015; McLennan et al., 2017; Strier, 2017). Although time budgets have been applied to assess primate behavioral flexibility to landscape change, the applications of these findings are largely limited to macaques (*Macaca sp.*) and baboons (*Papio sp.*) (McLennan et al., 2017). Anthropogenic assets such as high value food have been shown to decrease foraging time (Hoffman & O'Riain, 2011; Jaman & Huffman, 2013; Saj, Sicotte, & Paterson, 1999; Sha & Hanya, 2013) which often occurs in parallel with a decrease in movement (Jaman & Huffman, 2013; Wong & Candolin, 2015) and associated with an increase in social interactions (Jaman & Huffman, 2013; Saj et al., 1999; Scheun, Bennett, Ganswindt, & Nowack, 2015).

Seasonality is a strong predictor of time budgets in wild primates (Fan, Ni, Sun, Huang, & Jiang, 2008; Hendershott, Behie, & Rawson, 2016; Zhou et al., 2007), however, primates living in urban landscapes are often buffered against the effects of seasonality. Reports of seasonality on anthropogenically influenced monkeys are mixed. Some studies show no influence of seasonality, expressing this as a result of a continuous supply of high value resources available (Altmann & Muruth, 1988; Eley, 1989). Recent studies of more anthropogenically disturbed primates have shown that seasonality is influential on time allocation and suggest this to be an adaptive exploitive behavior (macaques; Jaman & Huffman, 2013, and baboons; Van Doorn, O'Riain & Swedell, 2010).

Prior research has assessed aspects of the landscape that influence the success and survival of vervet monkeys, *Chlorocebus pygerythrus*, in a modified anthropogenic environment (Chapman et al., 2016; Patterson, Kalle, & Downs, 2016). Although studies have considered time budgets of anthropogenically disturbed primates, no study has has yet assessed the flexibility in time budgets of an adapted generalist primate living in such a highly human populated urban setting. Furthermore, past research has only considered the consequences of either human/wildlife conflict (negative aspects) or access to high value resources (positive aspects) (McLennan et al., 2017). Studies examining the interaction between these negative and positive aspects are needed. As vervet monkeys continue to succeed in the ecologically developing urban landscape, the human wildlife conflict between vervet monkeys and local residents continues to grow with negative consequences for vervet monkeys (Wimberger, Downs, & Perrin, 2010; Wimberger & Downs, 2010). Vervet monkey population expansion in urban lansdscapes raises concerns both for vervet monkey wellbeing (Wimberger et al., 2010a,b) and ecological biodiversity conservation (Díaz, Fargione, Iii, & Tilman, 2006)

We aimed to investigate the effect of anthropogenic influences, both human food consumption (positive) and human-monkey conflict (negative) on the time budgets of vervet monkeys in an urban landscape. In order to do this, our main prediction focussed on ecological and landscape constraints. We predicted that anthropogenic disturbance would affect urban vervet monkeys' time budgets (Jaman & Huffman, 2013; Saj et al., 1999; Scheun et al., 2015). We predicted that positive anthropogenic aspects would decrease movement and foraging and increase social behavior as a trade off in time availability.

2. Methods

We conducted our study at Simbithi eco-estate, a private gated housing estate in Durban north coast, KwaZulu-Natal, South Africa (29.5140° S, 31.2197° E). The estate was previously two sugar cane farms that were developed 20 years ago to form a 430 ha estate (Simbithi eco-estate, 2017, pers. comm.). The estate was comprised of a variety accommodation options including apartment blocks, retirement complexes and general housing within a green mosaic. The estate had other anthropogenic leisure developments including restaurants, shops, fitness facilities, a golf course and a hotel. The estate encouraged wildlife research to help biodiversity management plans. Residents had mixed responses to vervet monkey presence ranging from actively encouraging vervet proximity to humans (intentional feeding by humans) to actively deterring vervet monkeys from human property (human aggression).

Vervet monkeys are commonly found in urban settings of KwaZulu-Natal (Thatcher, Downs, & Koyama, 2018) and therefore provided a candidate model to assess behavioral flexibility under anthropogenic changes (Chapman et al., 2016; Saj et al., 1999). The estate contained seven groups of vervet monkeys (Simbithi eco-estate, 2017, pers. comm.), although this study only considers the five groups that regularly stayed within the borders of the estate. Group size varied from 14-42 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). This was the first study on these groups so their history was unknown. Most monkeys were well habituated to humans due to the regular proximity to human residence. Two months were spent prior to commencing behavioral observations identifying. All adult vervet monkeys were identifiable via distinguishable markings, therefore, all 71 adult vervet monkeys were observed for this study.

We collected data from March 2016 - February 2017. We conducted observations from dawn until dusk (up to 8h in winter and 16h in summer) for a minimum of three weeks per month. Where possible we conducted a minimum of one observation per monkey per month, spread throughout the day (mean ± SD number of observations per group in the morning = 217 ± 33), midday = 251 ± 19 and afternoon = 286 ± 40). In total 3774 focal animal observations were conducted across all groups, averaging 650 ± 173 minutes per monkey.

We used focal animal sampling techniques (Altmann, 1974) to observe each individual for 20 min., sampling all group members before repeating observations in each month. We chose four key mutually exclusive categories to represent time budget foraging, movement, resting, social defined as foraging: a monkey actively searching for food items before feeding and directly consuming food items found (food items include, plants, aesthetic garden plants and human derived food) (Ménard et al., 2013; Saj et al., 1999); movement: included all types of locomotion not associated with any other activity, for example walking, running, climbing, and jumping (Ménard et al., 2013; Saj et al., 1999); resting: monkey in an inactive posture that excludes interacting with others, in a motionless position for longer than five seconds (Saj et al., 1999); social: monkey interacting with at least one other monkey including both affiliative and agnostic behaviors (Ménard et al., 2013; Saj et al., 1999).

During dawn until dusk follows of each group, 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 related possessions (car, house, bin etc.). For positive human incidents we included any form of human-food consumption (e.g. bread, fruit, pizza), an incident was classed as terminated once all human food was consumed, if the monkeys then obtained human food after 20 minutes we classed this as a new event. Negative human incidents were classed as any form of human-monkey aggression directed towards vervet monkeys (chase, rocks thrown etc.). Such interactions represent a cost to the vervet monkey due to the energy expended (running away) and 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 minutes. Positive and negative human incidents were not mutually exclusive, a human event could be coded twice as both positive and negative (e.g. monkey takes food from human house [positive] and is chased away [negative]). To support our monthly human values we also created an estimated monthly value of natural food availability. Following practiced phenology protocol we conducted five randomly placed walking transects within each group's home range noting all specimens $\geq$ 10cm diameter at breast height (Marshall & Wich, 2013). We retrospectively identified windows of fruit and flower availability using horticultural records for the region as in some previous studies (Blake, 1990; Wirminghaus, Downs, Symes, & Perrin, 2001). We split our data seasonally based on the four calendar seasons (summer: November-March, spring: September-October, autumn: April-June, winter: July-September) (SANBI, 2018).

2.1 Statistical analyses

For human values, we calculated a rate (frequency/month) per group based on how many incidents were observed according to hours of field observation each month. For behavioral observations we converted the total duration(s) of behavior to percentage of time spent performing that behavior per focal observation. Behavioral data were found to be not normally distributed using the Shapiro-Wilk's test ($p \leq 0.001$) (Ghasemi & Zahediasl, 2012). We calculated the variation inflation index of each predictor for inclusion in our model using the *car* package (Fox et al., 2007), setting the inclusion level at <3 (Zuur, Ieno, & Elphick, 2010). All data were analyzed using R statistical software (R project, 2013) and the significance level set at $p \leq 0.05$.

As data were non-parametric we ran a generalized linear mixed model on each behavioral category as the dependent variable using the *lme4* package (Bates, 2010). We created *a priori* maximum models that included positive human incidents, negative human incidents, natural food availability, group size and season as fixed effects. We controlled for repeated observations on individuals we included monkey identity as a random effect. Furthermore, we ran an interaction between positive and negative human incident rates. We scaled all our variables to produce a better fitting model. We ran all models with a gamma error distribution using a log link function.

To test whether the fixed effects explained variation we used a likelihood ratio test ('Anova' command set to "Chisq") comparing the maximum model against our null model (dependent variable plus one) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). If the maximum model was significantly better, we then ran a second likelihood ratio test on the maximum model to test the significance of each fixed effect (Zuur et al., 2009).

3. Results

3.1. Anthropogenic disturbance

The interaction effect between positive and negative human incidents showed that total time spent foraging was less when positive human incidents were low and negative human incidents were high, however a higher rate of positive incidents and less negative human incidents were related to an increase in time spent foraging (F_1=32.26, $p \leq 0.001$; Table 1, Fig.1a). The interaction between positive and negative human incidents showed that their movement increased as rate of positive human incidents decreased and the rate negative human incidents increased (F_1=3.9, $p = 0.045$; Table 2, Fig. 1b). Increased negative human incidents had a negative effect on time spent resting (F_1=12.29, $p \leq 0.001$; Table 3). The interaction effect between positive and negative human incidents showed that greater positive human incidents increased vervet monkey socializing time, but when they experienced both low negative and low positive human incidents their time spent socializing was significantly less (F_1=5.12, $p =$ 0.025; Table 4, Fig. 1c).

3.2 Group size

Vervet monkeys spent more time foraging with increasing group size (F_1=11.11, $p = 0.001$; Table 1). Vervet monkeys spent less time moving (F_1=38.19, $p \leq 0.001$; Table 2) and resting (F_1=7.43, $p = 0.006$; Table 3) with increasing group size.

3.3. Seasonality

Vervet monkey foraging was significantly affected by seasonality (F_1=96.79, p = $\leq$ 0.001; Table 1), with less time spent foraging in summer than any other season. In addition, their time spent moving (F_1=14.7, p = 0.002) and resting (F_1=64.41, $p \leq 0.001$; Table 3) was significantly affected by seasonality as vervet monkeys moved less and rested more in summer than any other season and more time resting in autumn than in winter and spring. Finally, their time spent socializing was also affected by seasonality (F_1=60.74, $p \leq 0.001$; Table 4) as this was significantly higher in summer than all other months.

[INSERT TABLE 1 HERE]

[INSERT TABLE 2 HERE]

[INSERT TABLE 3 HERE]

[INSERT TABLE 4 HERE]

[INSERT FIG. 1 HERE]

4. Discussion

As predicted, anthropogenic disturbance influenced all four aspects of the time budgets of urban vervet monkeys to some degree. Moreover, the interplay between positive and negative human incidents influenced three of the four behavioral categories. Results highlighted how urban vervet monkeys have adapted behaviorally to the ecologically changing anthropogenic landscape.

As expected, increasing anthropogenic food consumption by vervet monkeys significantly reduced their time spent foraging. Foraging results support previous research on provisioned vervet monkeys that high nutritional value human food provides more energy in smaller amounts in a shorter amount of time decreasing foraging requirements (Brennan, Else, & Altmann, 1985; Jaman & Huffman, 2013; Saj et al., 1999). The interaction effect between positive and negative human incidents showed that when positive incidents were low and negative incidents were high, vervet monkeys spent less time foraging, however, when positive human incidents were high and negative human incidents were low their foraging time increased. Notably, our interaction between positive and negative human incidents suggests that if vervet monkeys have access to high value anthropogenic food then despite human-aggression their time spent foraging will increase.

Time spent moving was greater when vervet monkeys experienced a higher rate of negative human incidents, although this effect decreased with more frequent positive human incidents. Previous research would suggest that access to high value resources should lessen the need to search for food and hence reduce time spent moving (Saj et al., 1999), supporting our findings. However, the interaction effect suggests that time spent moving is not only affected by successfully obtaining high value anthropogenic food resources, but is also associated with increased human aggression. Movement behavior therefore suggests that vervet monkeys may be less likely to move on in response to human aggression, when high value human foods are available, supporting recent findings by Thatcher et al (*in prep*).

Notably, vervet monkey social behavior increased with a greater rate of positive human incidents, supporting previous research, which has shown that access to high value food items results in decreased foraging time and increased time available for social behavior (Jaman & Huffman, 2013; Saj et al., 1999; Scheun et al., 2015). The negative interaction effect between both anthropogenic factors showed that negative human incidents offset this, decreasing social behavior. This could be due to the increased tension and aggression related to high value resources or as an outcome of human wildlife conflict (Fuentes & Hockings, 2010). It is possible that human-conflict affects social cohesion, however further study is required to investigate the impact of urban living on vervet monkey social systems and how both positive and negative associations affect social behavior both together and individually. Even so, as increased negative human incidents also reduced time spent resting, it could be suggested that human-aggression is generally costly to urban vervet monkey time budgets.

Although most historical research on urban primates has found no influence of seasonality (Altmann & Muruth, 1988; Eley, 1989), our research did show an effect of seasonality across all behaviors, supporting more recent studies that have shown that seasonality is still influential on urban species (Macaques: Jaman & Huffman, 2013 and Baboons: Van Doorn et al., 2010). Trends found followed expected patterns of energetic constraints (Borg et al., 2015; Mcfarland, Henzi, Barrett, & Wanigaratne, 2015). An unexpected finding was the seasonal effect of foraging. We expected that with access to high value food vervet monkeys would be less reliant on seasonally influenced natural food (Naughton-Treves, Treves, Chapman, & Wrangham, 1998), however, our results indicated that their foraging was significantly higher in autumn and winter. We suggest that this is due to a high reliance on attractive garden plants (Chaves & Bicca-marques, 2017; Hoffman & O'Riain, 2011; Kirsten Wimberger & Hill, 2017). Results for seasonality support previous research on urban baboons, showing how their adaptive generalist qualities have allowed them to take advantage of all aspects within their habitat (Fruteau, Voelkl, van Damme, & Noë, 2009; van Doorn et al., 2010). Seasonality results further highlights the exploitive nature of vervet monkeys and their behavioral flexibility, taking advantage of the most nutrient rich available resources, including seasonally influenced resources.

5. Management implications

Anthropogenic influences on the time budgets of vervet monkeys revealed independent and interlinking effects, which is a previously neglected area of ethnoprimatology research (McLennan et al., 2017). By developing our knowledge of urban ecology and behavioral adaptations, we can directly improve human-monkey relationships for the benefit of both parties through appropriate management plans (Soulsbury & White, 2015). We suggest that management should target preventing opportunities for vervet monkeys to forage on human food that which appear to drive human-monkey conflict. Housing estates should implement education programmes that encourage residents to reduce vervet monkey access to anthropogenic food availability (e.g. by securing refuse bins, reducing access points into houses, storing food items securely), with aim to reduce the human-wildlife conflict within urban areas for vervet monkey and human well-being, as well as ecological biodiversity conservation.

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Table 1

Output of GLMM and likelihood ratio test on urban vervet monkey foraging behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa.

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.05	0.20	15.20	≤0.001		
Negative human incidents	-0.69	0.18	-3.85	≤0.001	1.22	0.027
Positive human incidents	-1.10	0.15	-7.36	≤0.001	32.26	≤0.001
Negative human incidents * Positive human incidents	**1.04**	**0.22**	**4.78**	**≤0.001**	**22.84**	**≤0.001**
Group size	**0.02**	**0.01**	**3.33**	**0.001**	**11.11**	**0.001**
Natural food	**0.00**	**0.00**	**2.14**	**0.032**	**4.60**	**0.032**
Season					**96.79**	**≤0.001**
Autumn - Spring	**-0.31**	**0.10**	**-3.04**	**0.002**		
Autumn - Summer	**-0.82**	**0.10**	**-8.67**	**≤0.001**		
Autumn - Winter	0.04	0.09	0.40	0.687		
Summer - Spring	**0.52**	**0.08**	**6.36**	**≤0.001**		
Summer - Winter	**0.86**	**0.10**	**8.35**	**≤0.001**		
Spring - Winter	**0.34**	**0.09**	**3.73**	**≤0.001**		

Table 2

Output of GLMM and likelihood ratio test on urban vervet monkey movement behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa.

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.09	0.04	80.50	≤0.001		
Negative human incidents	0.10	0.02	5.41	≤0.001	24.72	≤0.001
Positive human incidents	0.21	0.02	11.54	≤0.001	40.86	≤0.001
Negative human incidents * Positive human incidents	**-0.03**	**0.02**	**-2.00**	**0.046**	**3.90**	**0.045**
Group size	**-0.18**	**0.03**	**-6.08**	**≤0.001**	**38.19**	**≤0.001**
Natural food	0.01	0.02	0.57	0.567	0.14	0.707
Season					**14.70**	**0.002**
Autumn - Spring	0.00	0.04	-0.02	0.986		
Autumn - Summer	**0.09**	**0.04**	**2.12**	**0.034**		
Autumn - Winter	-0.04	0.04	-1.10	0.273		
Summer - Spring	**0.09**	**0.03**	**2.73**	**0.006**		
Summer - Winter	**-0.13**	**0.04**	**-3.41**	**0.001**		
Spring - Winter	-0.04	0.04	-0.94	0.346		

Table 3

Output of GLMM and likelihood ratio test on urban vervet monkey resting behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa.

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	1.95	0.09	21.78	≤0.001		
Negative human incidents	**-0.15**	**0.05**	**-2.88**	**0.004**	**12.29**	**≤0.001**
Positive human incidents	0.04	0.05	0.70	0.483	0.56	0.451
Negative human incidents * Positive human incidents	-0.02	0.04	-0.45	0.654	0.20	0.655
Group size	**-0.12**	**0.04**	**-2.73**	**0.006**	**7.43**	**0.006**
Natural food	-0.05	0.05	-0.97	0.330	0.95	0.330
Season					**64.41**	**≤0.001**
Autumn - Spring	**0.27**	**0.12**	**2.18**	**0.029**		
Autumn - Summer	**0.81**	**0.11**	**7.35**	**≤0.001**		
Autumn - Winter	**0.26**	**0.12**	**2.12**	**0.034**		
Summer - Spring	**0.55**	**0.10**	**5.46**	**≤0.001**		
Summer - Winter	**-0.55**	**0.13**	**-4.36**	**≤0.001**		
Spring - Winter	-0.01	0.12	-0.08	0.938		

Table 4

Output of GLMM and likelihood ratio test on urban vervet monkey social behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.07	0.11	28.09	≤0.001		
Negative human incidents	-0.26	0.05	-5.29	≤0.001	55.28	≤0.001
Positive human incidents	0.09	0.06	1.61	0.108	3.15	0.08
Negative human incidents * Positive human incidents	**-0.09**	**0.04**	**-2.26**	**0.024**	**5.12**	**0.025**
Group size	0.02	0.08	0.19	0.850	0.04	0.850
Natural food	-0.08	0.05	-1.51	0.131	2.28	0.131
Season					**60.74**	**≤0.001**
Autumn - Spring	-0.08	0.12	-0.67	0.501		
Autumn - Summer	**-0.66**	**0.11**	**-5.84**	**≤0.001**		
Autumn - Winter	0.14	0.10	1.37	0.172		
Summer - Spring	**0.80**	**0.12**	**6.52**	**≤0.001**		
Summer - Winter	**0.74**	**0.11**	**-6.76**	**≤0.001**		
Spring - Winter	0.05	0.11	0.48	0.632		

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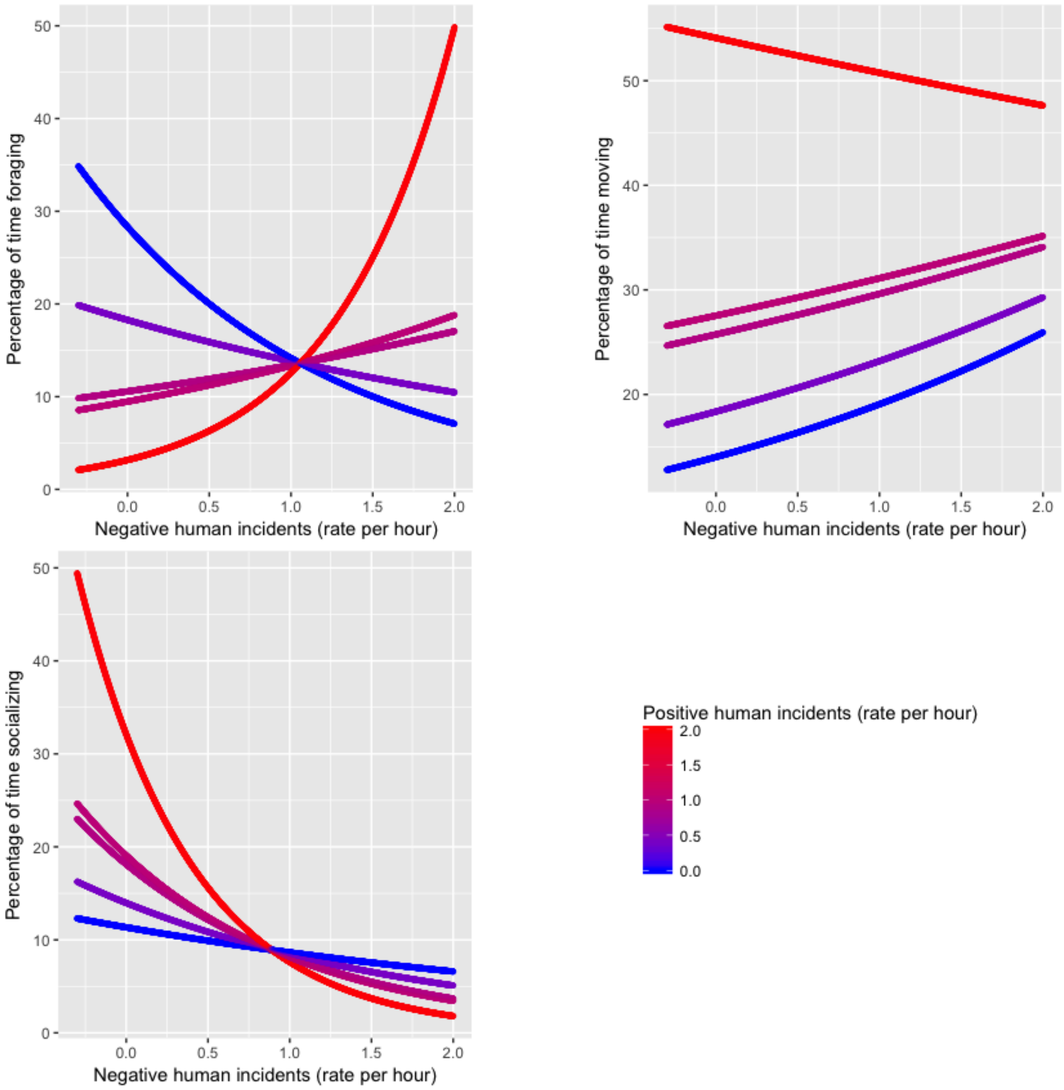
Fig. 1. Interaction between negative human incidents and positive human incidents on the time budgets of urban vervet monkeys at Simbithi Eco-estate, North Durban, KwaZulu-Natal, South Africa. (a) shows the positive significant effect on the percentage of time spent foraging, (b) shows the negative significant effect on the percentage of time spent moving and (c) shows the negative significant effect on the percentage of time spent socializing



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