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ORIGINAL ARTICLE

Sick and tired: sickness behaviour, polyparasitism and food stress in a gregarious mammal

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Abstract

Although sickness behaviour in response to non-lethal parasites has been documented in wild animals, it remains unclear how social and environmental stress might also shape an animal's behavioural response to parasitism, nor do we know whether simultaneous infection with more than one parasite changes the way animals respond. Here, we combine physiological, environmental, behavioural and parasite measures to investigate behavioural responses to infection in wild vervet monkeys (*Chlorocebus pygerythrus*) living in a semi-arid region of South Africa. We quantified both activity budget and behavioural predictability to investigate the occurrence of sickness behaviour and infection with two non-lethal gastrointestinal parasite genera. Higher parasite load was linked to an increase in the time spent resting. However, the nature of the relationship with other behaviours was contingent on both the parasite genus in question and parasite species interacted, highlighting the importance of considering co-infection. Overall, food availability was the dominant predictor of behavioural change suggesting that, for monkeys living in a more extreme environment, coping with ecological stress may override the ability to modulate behaviour in response to other physiological stressors. Our findings provide insight into how animals living in harsh environments find ways to cope with parasite infection, avoidance and transmission.

Significance statement

Sickness behaviour is a suite of behaviours that occur in response to infection that may serve as an adaptive response to cope with infection. For wild animals, the ability to express sickness behaviour will be modulated by the presence of other competing stressors. Hence, the patterns shown are likely to be more complex than under captive conditions, which is where most of our knowledge of sickness behaviour comes from. Using physiological, environmental, behavioural and parasite measures, we demonstrate that although vervet monkeys (*Chlorocebus pygerythrus*) living in a semi-arid region of South Africa do exhibit sickness behaviours, this is contingent on the parasite genus in question. Further, food availability was the dominant predictor of behavioural change suggesting that, for monkeys living in a more extreme environment, coping with severe ecological stress may override the ability to express sickness behaviour in an adaptive fashion.

Keywords Sickness behaviour · Primates · Gastrointestinal parasites · Semi-arid · Vervet monkey · Polyparasitism

Introduction

It has long been established that highly virulent parasites can drive population declines and may contribute to local extinctions (see: De Castro and Bolker 2005; Antonovics 2009; Best et al. 2012). Although often overlooked, the effects of subclinical or non-lethal infections can be costly to host health and fitness and consequently on population viability (Bohn et al. 2016). Hosts have evolved several physiological and behavioural responses to cope with the pressures of infection (Lopes 2014), and while we have

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some understanding of the physiological immune response to infections in animals, less is known about the behavioural presentation of sickness and its physiological correlates (Dantzer and Kelley 2007).

Sickness behaviour is very broadly defined as a suite of behaviours that occurs in response to infection. This includes lethargy, anorexia, somnolence and a reduction in grooming (Hart 1988; Dantzer and Kelley 2007). Although originally thought to be simply a by-product of infection, sickness behaviour is increasingly being considered to be part of a highly organised strategy to combat infection by reallocating energy to the immune system and away from non-essential activities (reviewed: Hart 1988; Aubert 1999; Johnson 2002). However, more work is needed to conclusively establish the adaptive nature of sickness behaviour in the wild (reviewed: Poulin 1995). If sickness behaviour is an inherently beneficial strategy to combatting infection, then a trade-off emerges as energetic resources are devoted to fighting infection at the expense of other vital processes, such as growth and reproduction (Lopes 2014). The severity of these costs, and hence the relative benefit of displaying sickness behaviour, depends on ecological context and the value of behaviours that need to be sacrificed. Thus, we should expect to see animals modulating their expression of sickness behaviours when the costs become too high. This is something particularly pertinent to animals subject to prolonged environmental or social stress given it is likely these animals have an already constrained activity budget and may not be able to express sickness behaviour even if it is beneficial (Cohn and de Sá-Rocha 2006; Moyers et al. 2015).

Sickness behaviour has been extensively documented in captive populations (Weary et al. 2009; Bohn et al. 2016; Lopes et al. 2016; Stockmaier et al. 2020), but we know much less about its occurrence in wild mammals (Krief et al. 2005; Ghai et al. 2015; Hamilton et al. 2020)—most likely due to the challenges associated with long-term environmental and physiological monitoring. Sickness behaviour research in the wild, therefore, has focused almost exclusively on the relationship between parasite infection and behaviour, independent of other stressors. However, the expression of sickness behaviour is more complicated if animals are simultaneously subject to other competing stressors common in natural environments (Cohn and de Sá-Rocha 2006; Moyers et al. 2015), and the expression of sickness behaviour should vary accordingly. Although we have some grasp of the social factors that influence investment in sickness behaviour (for review, see: Lopes 2014), the influence of environmental stressors remains poorly understood. Understanding the interplay between environmental stress and behavioural modification is central to understanding how sickness behaviour may impact long-term fitness in wild populations.

Sickness behaviour research has also been principally concerned with the effects of a single designated parasite or pathogen species on behaviour. Yet, wild animals rarely harbour only a single species, and interactions between parasite species are likely (Bordes and Morand 2011). This interaction can be either synergistic, where the parasite burden of one species magnifies the consequences of another, or antagonistic, where the burden supresses the other's effects (Graham 2008). At present, we have evidence that polyparasitism predicts infection risk (Telfer et al. 2010), host body condition and survival (Jolles et al. 2008) in mammals, but there is comparatively little research on how multi-parasite infection affects behaviour (see: Huffman and Seifu 1989; Huffman et al. 1993, 1997; Huffman 1997; Alados and Huffman 2000).

While sickness behaviour research generally focuses on activity or time budgets, there are other, more fine-grained, aspects of behaviour that may also be influenced by both physiological and environmental stress, including behavioural predictability and behavioural complexity. Unpredictable behaviour or complex behaviour is thought to be biologically adaptive as it allows organisms to cope with stress or unpredictable environments (Goldberger 1997; MacIntosh et al. 2011). A decrease in in the complexity of behavioural patterns has been linked to parasite infection in primates and may serve as a proxy measure of health suggesting the behavioural correlates of parasitism stretch beyond activity budget (see: Alados and Huffman 2000; MacIntosh et al. 2011; Ghai et al. 2015). Several measures of behavioural complexity have been used from the frequency of behavioural switching (Ghai et al. 2015) to long-range autocorrelation and fractal analysis (MacIntosh et al. 2011). Current measures used to quantify behavioural predictability and/or structure often require analytical restrictions being placed on the collected data. Typically, analysis is directed at two or three designated behaviours or at behaviours that have been combined into larger groupings. This is primarily due to the constraints of existing analyses and measures, which often require a single or a binary response variable. For example, MacIntosh et al. (2011) selected foraging and moving, from a broader range of possible behaviours, to assess the consequences of parasite infection in Japanese macaques, whereas to assess the health of chimpanzees, Alados and Huffman (2000) grouped all recorded behaviours into either social or nonsocial categories. A method of quantification that allows for the inclusion of more behaviours and/or a non-binary response may provide a broader insight into how animals respond and adapt to environmental changes and where the limits of these changes might lie.

One such measure is entropy rate which provides a way to combine behaviours into a discrete-time sequence

of distinct behaviours representing a stationary process in time (Davis et al. 2017). This allows more behaviours to be incorporated to quantify behavioural predictability, which reduces the analytical restrictions of the single or binary response measures previously mentioned.

Here, we use a comprehensive dataset composed of detailed physiological (faecal glucocorticoid metabolites), environmental, behavioural and parasite data to assess how these factors interact to shape behavioural responses to infection in a population of a highly social, wild mammal, specifically the vervet monkey (*Chlorocebus pygerythrus*), in a semi-arid region of South Africa. Previous work in this population has identified complex relationships between behaviour and environmental conditions, with food resources, temperature, rainfall and standing water availability strongly influencing activity budgets and mortality (McFarland et al. 2014; Young et al. 2019). As in this previous work, we use faecal glucocorticoid metabolites (fGCMs) as an index of individual response to environmental stressors (i.e. as a measure of the ability to restore homeostasis), rather than an indicator of an individual animal's stress levels (MacDougall-Shackleton et al. 2019). Given the often harsh environmental conditions in the study area, these monkeys provide an excellent opportunity to determine whether the expression of sickness behaviour occurs in wild animals that are subject to simultaneous external and internal stressors.

We use a combined approach, quantifying both activity budget and behavioural predictability, to investigate the relationships between behaviour and two non-lethal gastrointestinal parasite genera in the context of food stress. In addition to a more comprehensive dataset, we use a newly developed measure of entropy rate to assess predictability (Vegetabile et al. 2019); this allows a larger range of behaviours to be considered and may therefore be more sensitive than existing analytical techniques. Finally, we consider whether there is an interaction between the two parasite genera studied here and if co-infection compounds the need to invest in sickness behaviours.

Methods

Study site and study species

We collected behavioural data and faecal samples from April 2017 to March 2018 from three fully habituated groups (PT, Picnic Troop; RBM, River Bend Mob; RST, Riverside Troop) of wild vervet monkeys on Samara Private Game Reserve, South Africa (32°22′S, 24°52′E). These monkeys have been the subject of continuous data collection since 2009. All group members were individually identified based on natural markings, and data for this study were collected from a subset of 27 adult individuals (PT: 4 males, 6 females out of 14 adults; RBM: 2 males, 6 females out of 14 adults; RST: 3 males, 6 females out of 16 adults), selected to be representative of adult demography and to reflect the full range of dominance ranks. The study area comprises semi-arid riverine woodland (Pasternak et al. 2013), with a declining annual average rainfall of 386 mm, and average annual minimum and maximum temperatures of 10 °C and 27 °C, respectively. The region experiences periodic droughts that are severe enough to be a primary source of mortality for animals in our study groups (Young et al. 2019).

Behavioural data collection

Each group was followed for 5 days each week across the study period, and data were collected for 10 h each day (McFarland et al. 2015; Young et al. 2019). To assess changes in activity budget, the behaviour of all visible individuals was recorded during 10-min scan sampling blocks (Altmann 1974) conducted every 30 min throughout the day. We selected four, high frequency, mutually exclusive behaviours for analysis: moving, foraging, resting and allogrooming, either given or received. Notably, we considered foraging to include both manipulation and ingestion of food (for definitions, see: Isbell and Young 1993). It was not possible to record data blind because our study involved sampling individual focal animals in the field, which requires that researchers are able to recognise and follow a specific individual in the context of the social group. However, observers were "blind" to the parasite loads of the individuals from which data were collected, as all parasite analyses were conducted by RB once data collection in the field was completed.

To investigate changes in behavioural predictability, we conducted 10-min continuous focal sampling (Altmann 1974) twice per week for each of the 27 subjects ($N_{\text{total}} = 1614$ focal samples). Randomised focal times were generated for each day. During these focal sampling events, a single individual was followed and a continuous, timed record of its behaviour obtained, using electronic data loggers and proprietary software. The same mutually exclusive behaviours were identified as described above. Owing either to disruptions, such as aggressive encounters between groups, or periods where individuals were out of sight, not all focal samples were exactly 10-min long. To account for this, we controlled for focal sample length in our analyses, and the final dataset included focal samples where the individual was in sight for a minimum of 7.5 min.

Finally, we collected ad libitum data on dyadic agonistic interactions among all group members, for which we identified participants and outcomes. Given good visibility at the site, we are confident that there was no systematic bias in the likelihood of observing encounters. These agonistic data were used to construct dominance hierarchies (Young et al. 2019). Only decided dyadic agonistic interactions with a clear winner and loser were included in the analysis with the loser being defined as the last individual to show submission during the interaction.

Dominance hierarchy

We divided the study period into four 3-month blocks: April–June 2017, July–September 2017, October–December 2017 and January–March 2018. We used ad libitum observations of agonistic interactions to construct hierarchies for each period ($RBM_{\text{Total N}}$: 963; $RST_{\text{Total N}}$: 810; $PT_{\text{Total N}}$: 1135) for all adults in each troop and not only the subset of study subjects. Given male–female co-dominance in this population (Young et al. 2017b), we generated a single matrix that included all decided agonistic interactions regardless of the sex of participants and created a single interdigitated hierarchy.

Dominance ranks in each troop and for each 3-month block were expressed as a standardised David's score using the package "compete" (Curley 2016). David's scores were standardised to enable direct comparison across groups of different size and interaction rates (Henzi et al. 2013).

Food availability

We quantified food availability in each troop's home range by calculating the Normalised Difference Vegetation Index (NDVI) every 16 days (Young et al. 2019) from MODIS data collected by Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1). Using Moderate Resolution Imaging Spectroradiometer MOD13Q1 vegetation indices at a 250-m resolution (Didan 2015), the NDVI measures the amount of biomass or chlorophyll activity by calculating the difference between the visible red and near infrared bands divided by their sum. The resultant measure is a range of values between − 1 and 1, where negative values indicate an absence of vegetation and positive values approaching 1 indicate larger concentrations of green vegetation (Pettorelli et al. 2005). Given the generalist, largely plant-based nature of vervet diet (Pasternak et al. 2013), the synoptic view of the NDVI is a reliable measure of food availability in this species and at this site (Willems et al. 2009; Jarrett et al. 2020).

Faecal sampling and analysis

We collected a total of 573 faecal samples (mean = 21/individual, ± 3.1 *SD*) during the 234 days of the study. Faecal samples were collected twice per month (once during each 2-week period) from the 27 subjects. Two corresponding faecal samples, one for parasite analysis and one for faecal glucocorticoid metabolites (fGCM) analysis, were collected from the same defaecation event.

Parasite analysis

For each sample, approximately 1 g of fresh faeces was weighed in the field immediately after defaecation and directly placed into 10% neutral, buffered formalin. Samples were stored in the field lab and transported to the University of Lethbridge, Canada, where faecal flotation and sedimentation techniques were used to identify parasites (Blersch et al. 2019).

We used a modified zinc sulphate flotation to isolate helminth eggs followed by ethyl-acetate sedimentation to isolate potential trematodes that were too heavy to float during ZnSO4 flotation (methods: supplementary S1). For both methods, the entire pellet was examined under the microscope. Parasites were identified to genus level based on egg shape, size, colour and contents, and all eggs were counted. Representative eggs were photographed.

We recovered 5 parasite genera from faecal samples (Blersch et al. 2019). One parasite could not be identified to genus level, as eggs of *Physaloptera* sp. and *Protospirura* sp. cannot be reliably distinguished based on egg morphology alone. Based on morphological characteristics of the eggs, including their size and the presence of a hyaline substance (Brumpt 1931; Petrželková et al. 2006), we consider it most likely to be *Protospirura* sp. (hereafter referred to as ?*Protospirura* sp.) pending results of ongoing molecular analysis. Preliminary molecular analyses suggest the parasite is a single species. Due to small sample size for three genera (< 5% mean annual sample prevalence), namely *Oesophagostomum* sp., *Subulura* sp. and *Ternidens* sp., we selected only ?*Protospirura* sp. and *Trichostrongylus* sp. (> 20% mean annual sample prevalence) for these analyses but include other genera in the number of genera (parasite richness).

We have established previously that sequential faecal egg count patterns for *Trichostrongylus* sp. and ?*Protospirura* sp. are not stochastic and point to underlying levels of infection in our population (Blersch et al. 2021) and thus use egg counts as a proxy for the extent of helminth infection.

Faecal steroid analysis

Samples were collected following the protocol of Young et al. (2017a, 2019). Within 15 min of defaecation, a 2–5-g piece of faecal material was transferred into a plastic vial following physical homogenisation of the full faecal sample. Prior to collection, faecal samples were checked to ensure there was no contamination with urine during excretion or on the substrate where the sample landed. Vials were immediately stored on ice in a thermos flask in the field before transfer to a − 20 °C freezer at the end of the day. Samples were stored frozen until transport on dry ice to the Endocrine Research Laboratory, University of Pretoria, for analysis.

Samples were lyophilised, pulverised and then sieved to remove seeds and fibrous matter (Young et al. 2017a). The resulting faecal powder (0.10 g) was extracted by vortexing for 15 min with 80% ethanol in water (3 ml) followed by 10 min of centrifugation at 1500 g. A total of 1.5 ml of the resultant supernatants were transferred into microcentrifuge tubes. Hormone analysis was conducted following the standard procedures of the Endocrine Research Laboratory, University of Pretoria (Ganswindt et al. 2002), using the cortisol enzyme immunoassay (EIA) (Young et al. 2017a). The sensitivity of the EIA used was 0.6 ng/g dry weight (Young et al. 2017a). Inter- and intra-assay coefficients of variation of high- and low-value quality controls were: 4.64–5.96 and 8.13–11.60%, respectively. All steroid concentrations are given as ng g^{-1} faecal dry weight.

Applying entropy rate to the behaviour of free-ranging animals

Entropy rate has been successfully applied to quantify the predictability of maternal signalling in captive mice but has not been tested in the wild (Vegetabile et al. 2019).

To determine whether entropy rate can be applied to our observed data, and to get a sense of the sensitivity of the measure, we simulated a dataset that closely matched our observed data. Simulated data allowed us to make specific predictions related to the influence of environmental conditions on behavioural predictability where the outcome is already known. As entropy rate has only been applied narrowly in the field of animal behaviour research, this functioned as a test of whether the entropy rate measure is capable of retrieving the known outcome in simulated behavioural data comparable to wild vervet monkey behaviour. If the outcome can be successfully retrieved in simulated data, entropy rate can then be reliably applied to explore general relationships between social and environmental factors on behavioural predictability in the wild. Furthermore, simulation provides control over the magnitude of behavioural change in response to environmental change which serves as a coarse measure of the sensitivity of entropy rate to capture changes in behavioural predictability.

We derived the simulation from the prediction that an increase in food availability was associated with a reduction in time spent foraging and a consequent increase in the time spent engaged in social behaviours. First, we simulated a range of NDVI values between 0.25 and 0.6, which was consistent with our observed data. Then, we simulated behavioural sequences across NDVI values, while keeping the sequence length ($n = 20$ behaviours) associated with the greatest variance, number of focal samples ($n = 1553$) and number of individuals ($n = 27$) consistent with our observed behavioural data. Given that our observed dataset extends predominantly through summer, we started with an activity budget similar to the probabilities of behaviours found during the hot-dry period by Young et al. (2019). We then simulated data such that the time spent foraging decreased with increasing NDVI, using a low (2%), medium (7%) or high (20%) decrease in foraging time between minimum NDVI and maximum NDVI. We then calculated the entropy rate for each generated sequence. This range served as an indicator of how much entropy rate can be expected to vary in relation to the magnitude of behavioural change, thus providing a coarse measure of sensitivity. For modelling purposes, we then selected sequences derived from a 7% change in foraging time based on previous estimates of seasonal variation in foraging time (Young et al. 2019). These simulated data were used in a Bayesian mixed-effects model (brms package Bürkner 2017, 2018) to test our prediction that an increase in NDVI would result in a decrease in entropy rate. We used NDVI as our fixed effect and individual ID as our random effect. Other variables, such as troop ID or dominance rank, were not used in this model as our primary interest was whether we could retrieve the known influence of NDVI on entropy rate while aiming to keep the simulation as clear and simple as possible.

Entropy rate: time interval selection

In order to estimate entropy rate, continuous focal samples had to be discretised into coded behavioural sequences. We therefore first determined the sampling time interval that resulted in maximum variance across sequences. This ensured that our measure was sensitive enough to detect small changes in behaviour. We assigned each behaviour a single letter and created coded behavioural sequences by extracting behaviour from each focal at 3-s, 5-s, 10-s, 15-s, 20-s, 30-s, 45-s, 60-s, 90-s, 120-s and 300-s intervals. This generated 11 sets of sequences for each focal that ranged from 2 to 200 consecutive behaviours. We then used the entropy package (Hausser and Strimmer 2014) in R version 3.4.4 (R Core Team 2018), to calculate the entropy rate, together with the variance and standard deviation (SD) for

each sequence for each time interval. A sampling interval of 30 s resulted in maximum variance ($Var = 0.157$) across sequences, and we therefore used sequences from a 30-s sampling interval for further analysis.

Statistical analysis

Patterns of co-infection

Egg counts of our two most prevalent parasite genera, ?*Protospirura* sp. and *Trichostrongylus* sp., were used in these analyses. We conducted exploratory analysis to assess whether there was a relationship in parasite intensity between ?*Protospirura* sp. and *Trichostrongylus* sp., using a mixed-effects model in a Bayesian framework and specifying a lognormal distribution. We filtered out samples that were parasite negative ($N = 8$). ?*Protospirura* sp. intensity, represented as eggs per gram (EPG), was our response variable, while *Trichostrongylus* sp. was our fixed effect. We included individual ID nested in troop as our random effect with individual-level random slopes for *Trichostrongylus* sp.

Model set 1: the influence of parasite infection and ecology on behaviour

To examine whether infection with ?*Protospirura* sp. and *Trichostrongylus* sp. and parasite species richness (the number of genera recovered in each faecal sample) were associated with changes in behaviour, we used scan data ($N_{scans} = 27{,}068$) to construct a multilevel multinomial behavioural model (Koster and McElreath 2017) with the Rstan package (Stan Development Team 2020). We linked 1 week of behavioural data (3 days before the faecal sample collection and 4 days after) to each faecal sample for the corresponding individual for both parasite data (Ghai et al. 2015) and fGCM concentrations. We found no qualitative differences in estimates between the reduced and full focal datasets for the variables that could be included (results: supplementary S2).

Multilevel, multinomial behavioural models estimate the likelihood of a given behaviour from a set of categorical behaviours occurring at any given time in relation to a reference behaviour, while controlling for repeated observations from the same individual.

We set behaviour (feeding, resting, grooming given, grooming received and moving) as our response variable, with moving as our reference variable. Moving was selected, as the reference variable is sensitive to frequency, and moving is a very common behaviour. We included parasite intensity (given as eggs per gram), parasite richness (number of genera) and NDVI as our primary fixed effects. We also controlled for other physiological effects by including fGCMs as a fixed effect, and we also controlled for sex, standardised rank and date. Individual ID and troop were included as random effects. In addition to summary statistics, we generated predicted probabilities for each behaviour for each predictor variable while holding other coefficients constant. This allowed us to look at changes in all behaviours, including the reference variable. Owing to the use of a reference behaviour (i.e. moving), coefficients of the multinomial model are not straightforward indicators of the effect of a predictor on the probability of performing a given behaviour (Koster and McElreath 2017); thus, predicted probabilities are computed to understand the effects of the fixed effects on each behaviour.

Model set 2: the influence of parasite infection and ecology on behavioural predictability

We used entropy rate to determine whether parasite infection affects behavioural predictability. Entropy rate quantifies the predictability of the next observation, given the history of observations which occurred before it. Our entropy rate method estimates the distribution of behaviours (the frequency of each) and a transition matrix that describes transitions between behaviours (Vegetabile et al. 2019). An entropy rate of zero would indicate an individual engaged in a single behaviour for the entire observation period, whereas an entropy rate of 1 indicates that an individual, either engaged in multiple behaviours, switched behaviours frequently or both. As entropy rate has only been applied narrowly in animal behaviour, we began by validating its extension to observational data from wild monkeys, using both simulated and observed data (methods and results: supplementary S3). In order to estimate entropy rate, continuous focal samples were discretised into coded behavioural sequences. We assigned each behaviour a single letter code and created behavioural sequences by extracting behaviour from each focal at 30-s intervals, the optimal time period identified ($N = 693$ faecal sample-matched sequences). We then used the "entropy" package (Hausser and Strimmer 2014) in R version 3.5.2 (R Core Team 2018), to calculate the entropy rate.

Bayesian mixed-effects model structure

We constructed a mixed-effects model with a Gaussian distribution in a Bayesian framework to assess the relationship between parasite intensity and behavioural entropy rate (distribution comparison results: supplementary material S4). Our response variable was behavioural entropy rate and, as with model 1, parasite intensity for ?*Protospirura* sp. and *Trichostrongylus* sp., parasite richness and NDVI were included as our primary fixed effects while controlling for fGCM concentration, rank and sex as fixed effects. Given

that individuals may be more likely to be active earlier in the morning and resting or grooming during the hottest part of the day, which may affect behavioural predictability, we included a spline on time of day as a fixed effect. Individual ID and troop were included as random effects. As not all focal samples were exactly 10-min long, we also controlled for sequence length. We standardised continuous variables (rank, NDVI and sequence length) using one standard deviation (SD) to allow comparisons of effect sizes across continuous and dichotomous variables. These variables were mean-centred on zero. We ran models with 4 chains and 2000 iterations which allows for a large enough sampling pool to achieve model convergence and conduct posterior sampling (McElreath 2016; Bürkner 2018). We used weakly informative priors (normal (0, 1)), and chain convergence was confirmed by $\hat{R}$ values ≤ 1.01. Model goodness-of-fit was assessed using the "posterior predictive check" (pp_check) function in the "bayesplot" package (Gabry et al. 2019).

Results

Using entropy rate to quantify behavioural predictability in wild primates

We found that entropy rate can be used to quantify behavioural predictability in our population. Using a 30-s sampling interval, mean entropy rate in our population was 0.76 (± 0.40 *SD*).

Based on simulated data, we found that behaviour became more predictable as NDVI increased and the proportion of time spent foraging decreased. This indicates that entropy rate successfully captures changes in behavioural predictability in data of similar structure to our observed data. Regarding sensitivity, when considering the magnitude of behavioural change required to detect a change in entropy rate, simulation showed that a 2% decrease in foraging between minimum and maximum NDVI does not result in a reliable change in entropy rate, while we may expect a change in entropy rate of approximately 0.3 with a 19% decrease in foraging and increase in social interactions.

Patterns of infection and co-infection

?Protospirura sp. had a mean annual sample prevalence of 98.74% (± 1.74 *SD*) and host group prevalence of 99.33% (± 1.51 *SD*) with only 8/573 samples negative for all parasites. *Trichostrongylus* sp. had a mean annual sample prevalence of 22.04% (± 17.56 *SD*) and host group prevalence of 25.69% (± 17.53 *SD*). Thus, all samples that were positive for *Trichostrongylus* sp. were also ?*Protospirura* sp. positive.

For ?*Protospirura* sp., annual minimum and maximum egg counts from positive samples (ps) were 2 eggs per gram (EPG) and 5841 EPG, respectively ($mean_{ps}$ = 752.22 ± 861.33 *SD*, $median_{ps}$ = 425.75), while for *Trichostrongylus* sp., egg counts ranged from 2 to 47 EPG ($mean_{ps}$ = 6.5 ± 5.29 *SD*, $median_{ps}$ = 5.28).

We found no evidence of a population-level relationship between ?*Protospirura* sp. infection intensity and *Trichostrongylus* sp. infection intensity (Estimate = 0.39, Estimate error = 0.63, lower 95% credible interval = − 0.98, upper 95% credible interval = 1.56).

We found some evidence of inter-individual differences in random slopes for co-infection patterns of parasite intensity (Fig. 1). For some individuals, infection intensity of ?*Protospirura* sp. was high when *Trichostrongylus* sp. was absent or intensity is low. However, when *Trichostrongylus* sp. infection intensity was higher, ?*Protospirura* infection intensity was also high for some individuals. This pattern is stronger for some individuals than others. Note that estimate uncertainty is high for some individuals due to smaller individual-level sample size, and this result should be interpreted with caution. Full model results are provided in the supplementary material (S5.1) and a version of Fig. 1 including credible intervals is also provided in the supplementary material (S5.2).

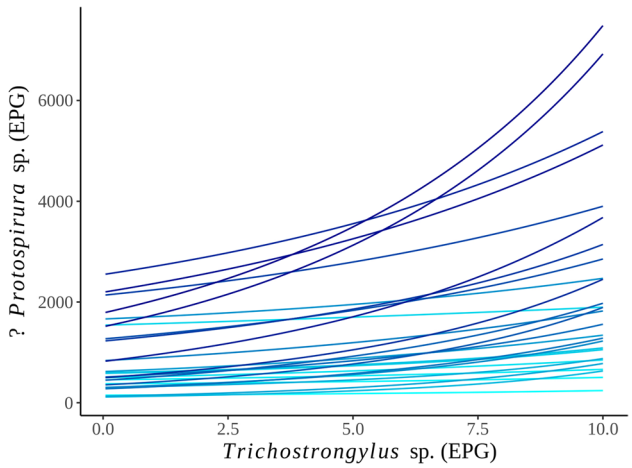

Fig. 1 Individual-level estimates of faecal egg count (eggs per gram, EPG) of ?*Protospirura* sp. as a function of *Trichostrongylus* sp. faecal egg count derived from the fitted Bayesian mixed-effects model. Dark blue lines show individuals with a strong positive relationship between *Trichostrongylus* sp. and ?*Protospirura* sp. Upper and lower 95% credible intervals excluded for clarity

Model set 1: influence of parasite infection and ecology on behaviour

Fixed effects

We found evidence of parasite-induced lethargy (i.e. increased resting time) and anorexia (i.e. reduced feeding time) as ?*Protospirura* sp. egg count increased (Fig. 2a). The probability of resting increased by 8.7% (*l-CI* = 2.2, *u-CI* = 14.9) when egg counts were highest. This was predominantly traded off against moving, which showed a 7.4% decrease (*l-CI* = 2.9, *u-CI* = 12.2), and there was also a 4.3% decrease (*l-CI* = 0.16, *u-CI* = 8.3) in the probability of foraging. The probability of both giving and receiving grooming were largely unchanged.

Conversely, we found that an increase in *Trichostrongylus* sp. loads resulted in a 15.4% (*l-CI* = 6.3, *u-CI* = 24.6) reduction in the probability of resting. There was also an 8.8% (*l-CI* = 0.2, *u-CI* = 21.1) increase in the probability of foraging, while the probability of moving remained largely unchanged (Fig. 2b). The probability of both giving and receiving grooming increased slightly, by 4.0% (*l-CI* = −0.8, *u-CI* = 17.8) and 3.04% (*l-CI* = −1.6, *u-CI* = 11.4), respectively, when *Trichostrongylus* sp. egg counts were higher; however, credible intervals were wide indicating uncertainty.

An increase in parasite species richness resulted in a slight decrease in the probability of resting (4.2%, *l-CI* = −1.7, *u-CI* = 10.4). However, credible intervals were wide and uncertainty high. Parasite richness did not influence the probability of the other behaviours occurring (Fig. 3a).

Although parasite intensity predicted changes in activity budget, the strongest predictor was change in food availability (Fig. 3b). When food availability was high, the probability of foraging decreased by 18.4% (*l-CI* = 12.3, *u-CI* = 23.8). This was accompanied by a 12.3% (*l-CI* = 8.1, *u-CI* = 16.0) increase in the probability of resting and a 10.1% (*l-CI* = 5.5, *u-CI* = 14.8) increase in the probability of moving. The probability of grooming given and received decreased slightly by 2.1% (*l-CI* = 0.09, *u-CI* = 7.9) and 1.9% (*l-CI* = 0.6, *u-CI* = 4.4), respectively. The full model output and summary can be found in the supplementary material (S6).

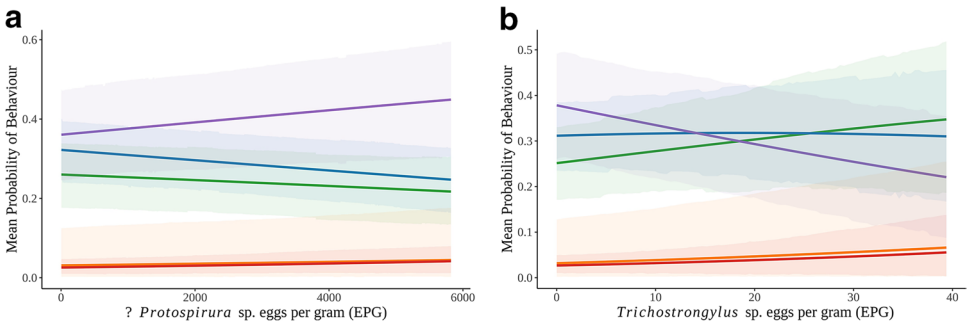

Fig. 2 The relationships between the probabilities of behaviours being expressed as a function of **a** ?*Protospirura* sp. (EPG) and **b** *Trichostrongylus* sp. (EPG). The 5 behaviours are foraging (green), resting (purple), moving (blue), grooming in (red) and grooming out (orange). Shaded regions show 89% percentile intervals as calculated from the posterior samples

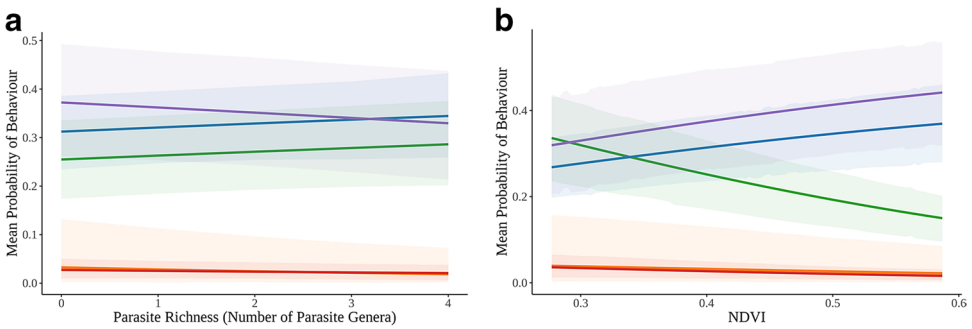

Fig. 3 The relationships between the probabilities of behaviours being expressed as a function of **a** parasite richness and **b** food availability (NDVI). The 5 behaviours are foraging (green), resting (purple), moving (blue), grooming in (red) and grooming out (orange). Shaded regions show 89% percentile intervals as calculated from the posterior samples. NDVI, Normalised Difference Vegetation Index

The influence of co-infection on behaviour

We found that, when *Trichostrongylus* sp. infection intensity was low (2 EPG), the probability of resting increased, feeding decreased and moving decreased as ?*Protospirura* sp. egg count increased (Fig. 4). When *Trichostrongylus* sp. was high (35 EPG), the mean probability of resting was lower overall but still rose with increasing ?*Protospirura* sp. egg count and the probability of foraging decreased further. The probability of moving remained the same.

Model set 2: influence of parasite infection and ecology on behavioural predictability

We found evidence of a positive relationship between NDVI and entropy rate (Table 1). This indicates that an increase in food availability was associated with a decrease in behavioural predictability. We found some evidence of a non-linear relationship between entropy rate and time of day (*sds est.* = 0.27, *est. error* = 0.23, *l-CI* = 0.01, *u-CI* = 0.89) where sds is the spline variance parameter. Behavioural predictability was lowest in the early morning and increased until mid-day (Fig. supplementary S7).

We found no evidence that ?*Protospirura* sp. and *Trichostrongylus* sp. parasite intensity or parasite richness influenced entropy rate (Table 1). Similarly, fGCM concentration, sex, rank and individual ID did not influence behavioural predictability. We found no effect of sequence length on entropy rate, which supports our use of focal samples exceeding 7.5 min. The full model only explained 9.2% of variance ($R^2 = 0.09$, *est. error* = 0.02, *l-CI* = 0.06, *u-CI* = 0.13) suggesting there are other underlying drivers of behavioural predictability.

We found some evidence of a small, positive interaction between ?*Protospirura* sp. intensity (EPG) and *Trichostrongylus* sp. intensity. When *Trichostrongylus* sp. was low (2 EPG), entropy rate decreased with increasing ?*Protospirura* sp. intensity (Fig. 5). Conversely, when *Trichostrongylus* sp. egg count was high, entropy rate increased with increasing ?*Protospirura* sp. infection intensity.

Discussion

Our results showed a relationship between parasite intensity and behavioural change, providing evidence for sickness behaviour in vervet monkeys. The nature of this relationship was not straightforward, however: we found that higher parasite loads predicted an increase in time spent resting but that other behavioural changes were contingent on both the parasite genus in question and their interactions. This highlights the benefit of considering multiple parasite infections when assessing the links between behaviour and infection in wild non-human primates. Although we found evidence for changes in the overall amount of time devoted to particular activities, we found only limited evidence for more fine-grained changes in behavioural predictability (i.e. behavioural entropy rate) in response to increased parasite

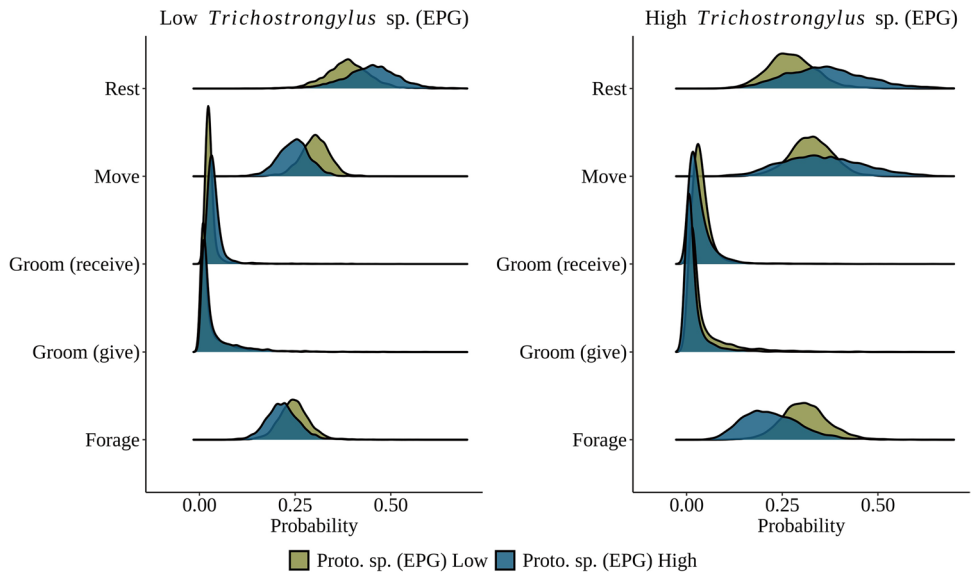

Fig. 4 Changes in the mean probability of behaviours in response to high ?*Protospirura* sp. (Proto. sp.) when *Trichostrongylus* sp. intensity (EPG) was low (green) and high (blue). Density plots show probability of behaviours predicted by the model, with the height of the density curve indicating the probability of the predicted behaviour. The spread of the curve indicates the uncertainty. Egg counts are continuous variables in the model and are categorised as "high" and "low" for visualisation purposes only. This was to aid in interpretation only, and no assumptions was made about as to the biological significance of what is designated as "high" or "low"

Table.1 Summary statistics of generalised additive mixed-effects model examining the influence of parasite infection and social factors on entropy rate

		Effect	Estimate	Est. error	l-95% CI	u-95% CI	*R″*
Fixed effects	Population-level	Intercept	0.81	0.09	0.61	1.01	1
		?*Protospirura* sp. (EPG)	−0.04	0.04	−0.11	0.03	1
		Trichostrongylus sp. (EPG)	−0.06	0.06	−0.17	0.05	1
		Interaction (*Proto.* sp.Trich.* sp.)**	**0.08**	**0.04**	**0.01**	**0.16**	**1**
		Parasite richness (no. of genera)	−0.03	0.04	−0.11	0.05	1
		NDVI	**0.1**	**0.03**	**0.03**	**0.16**	**1**
		fGCM concentration	−0.01	0.03	−0.07	0.05	1
		Sex (ref: male)	−0.03	0.04	−0.1	0.05	1
		Rank	0.03	0.04	−0.05	0.1	1
		Sequence length	−0.05	0.03	−0.11	0	1
		Time of day (spline)	−0.32	0.46	−1.24	0.7	1
Random effects	Smooth Terms ID	sds (sTime of day)	0.27	0.23	0.01	0.88	1
		SD (intercept)	0.04	0.02	0	0.09	1
	Troop	SD (intercept)	0.09	0.11	0	0.42	1
Family		Sigma	0.38	0.01	0.36	0.4	1

CI, credible interval; *SD*, standard deviation. Smooth-term sds() = spline "wiggliness"(spline variance parameter)

$R^2 = 0.09$, *est. error* = 0.02, *l-CI* = 0.05, *u-CI* = 0.13

Estimates for fixed effects where credible intervals do not cross zero are in bold

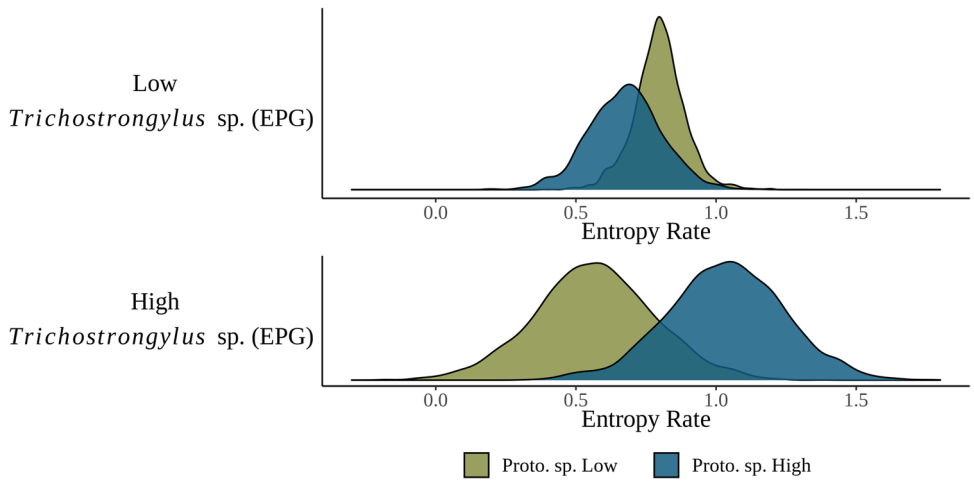

Fig. 5 Changes in entropy rate in response to high ?*Protospirura* sp. (Proto. sp.) when *Trichostrongylus* sp. intensity (eggs per gram, EPG) was low and high. Density plots show entropy rate predicted by the model, with the height of the density curve indicating the probability of the predicted entropy rate. The spread of the curve indicates the uncertainty. Egg counts are continuous variables in the model and are categorised as "high" and "low" for visualisation purposes only. This was to aid in interpretation only, and no assumptions was made about as to the biological significance of what is designated as "high" or "low"

intensity. Given that food availability was the best overall predictor of behavioural change, it is likely that, for monkeys living in more extreme environments, coping with ecological stress overrides any fine-scaled ability to modulate behaviour in response to other stressors.

In line with previous work on non-human primates (Huffman et al. 1996; Huffman 1997; Huffman and Caton 2001; Ghai et al. 2015; Friant et al. 2016), we found evidence of sickness behaviour in response to two non-lethal gastrointestinal parasite infections. We found that increases in parasite intensity (EPG) of both ?*Protospirura* sp. and *Trichostrongylus* sp. were linked to changes in activity budget suggesting that these monkeys modify their behaviour in response to high parasite infection load. High ?*Protospirura* sp. parasite

intensity resulted in "typical" sickness behaviour—increased resting and reduced foraging and moving. This is notable as ?*Protospirura* sp. transmission relies on an intermediate arthropod host, so we might expect a positive relationship between foraging and increased parasite load. The inverse relationship in this case provides further support for the idea that what we see here is, indeed, sickness behaviour. It is possible that the change in behaviour is due to other underlying physiological processes that also occur when ?*Protospirura* sp. infection intensity is high. However, we found no relationship between fGCM concentration and behaviour, suggesting that changes in behaviour may be a result of gastrointestinal parasite infection rather than an indication that individuals are coping with other stressors. Still, it is possible that this lack of relationship may also be a result of fGCM data collection not being fine-grained enough and a failure to detect more short-term increases in fGCMs. This emphasises the value of considering multiple physiological variables in assessing parasite-host relationships.

In the case of *Trichostrongylus* sp., we found a different pattern, where high infection intensity was associated with an increase in the amount of time spent foraging, along with a decrease in the probability of resting. The implication here is that different gastrointestinal parasites may exert different physiological pressures on the host and the manner in which they successfully cope with different non-lethal infections. For example, nutrition plays a vital role in a host's ability to cope with the negative effects of gastrointestinal parasites (Ezenwa 2004), which could result in the need to forage more when *Trichostrongylus* sp. infection is high. Alternatively, high *Trichostrongylus* sp. parasite intensity may coincide with other environmental or social changes that influence host behaviour or parasite dynamics. We found no relationship between temperature, rainfall or NDVI and *Trichostrongylus* sp. parasite intensity (Blersch et al. 2021), suggesting that monkeys are not simply foraging more when *Trichostrongylus* sp. is high because food availability is lower. It is also possible that, given the relatively low egg counts of *Trichostrongylus* sp., individuals may not have been harbouring sufficiently high parasite burden to elicit typical sickness behaviour.

We were also able to consider the co-occurrence of the two parasites. We found no strong relationship between *Protospirura* sp. and *Trichostrongylus* sp. faecal egg counts indicating that there is neither a synergistic nor antagonistic relationship between these two parasites, which further suggest there is no direct competition between them (Bordes and Morand 2011). There were differences in egg counts with ?*Protospirura* sp. egg counts being both higher and more variable than *Trichostrongylus* sp. egg counts. We did find, however, that co-infection with these two nematodes was linked to different activity budget changes. When parasite intensity was high for both species, shifts in behaviour were different from those seen when only a single infection was considered. Specifically, we found that, when *Trichostrongylus* sp. infection intensity was high, monkeys still rested more with increasing ?*Protospirura* sp. egg count (i.e. showed the same pattern as when we considered ?*Protospirura* sp. infection alone), but they also moved more and decreased foraging further, which contrasts with the findings for ?*Protospirura* sp. alone. While the presence of both infections may also be linked to external environmental or social changes, it lends support to the hypothesis that multiple infections exert differential changes on the wild host (reviewed: Bordes and Morand 2011) and highlights the need to address co-infections when assessing animal health.

Contrary to some previous work on bats (Stockmaier et al. 2018, 2020) and non-human primates (Ghai et al. 2015), we found no marked change in the probability of either giving grooming or receiving grooming for individual infections and only a small reduction in allogrooming when both ?*Protospirura* sp. and *Trichostrongylus* sp. infection intensity were high. While investment in sickness behaviour may be fundamentally beneficial, and suppression of sickness behaviour may be detrimental to host fitness and survival, animals have to weigh the cost of modulating behaviours in response to infection (Lopes 2014). Minimal change in grooming in relation to infection intensity suggests these vervets maintain social relationships in the face of such external pressures. Young et al. (2019), however, found that vervets engaged in fewer social behaviours when environmental conditions were suboptimal. Given the harsh semi-arid environment, these vervets may be unable to further reduce the amount of time spent grooming in response to parasite infection; that is, they may have already reduced their grooming investment to the extent that any further reductions would incur unsustainable costs with respect to individual social benefits and/or to group cohesion (Cohn and de Sá-Rocha 2006; Moyers et al. 2015).

While our focus here was solely on time spent grooming, social interaction has been linked to infection susceptibility and transmission in several social species (Otterstatter and Thomson 2007; Drewe 2010; Briard and Ezenwa 2021) including non-human primates (Wren et al. 2015; Romano et al. 2016). This suggests that, despite the lack of change in the time spent grooming, increased parasite load may result in alternative suppressive strategies, such as changes in the number or identity of grooming partners. However, these strategies may be contingent on the route of parasite transmission which, for ?*Protospirura* specifically, is unlikely to be from direct transmission between individuals. More detailed grooming analysis is required to fully understand whether these vervets do, at least in part, modulate their grooming behaviour in response to infection and the risk that maintaining grooming frequency may incur. Alternatively, the relationship

between grooming and parasite infection simply may be less clear given the lower time invested in grooming in comparison to other behaviours.

We also considered whether parasite infection intensity was linked to changes in behavioural structure. Behavioural entropy rate, derived from focal data, was not linked to individual parasite infections, but, when *Trichostrongylus* sp. infection intensity was high, entropy rate increased with increasing ?*Protospirura* sp. egg shedding. Thus, polyparasitism was associated with decreased behavioural predictability, indicating that monkeys engaged in more behaviours, changed behaviours more frequently or both. This contrasts with studies on non-human primates that found a reduction in behavioural complexity or the rate of behavioural switching when individuals were parasite positive (Ghai et al. 2015) or had impaired health (Alados and Huffman 2000; MacIntosh et al. 2011). Given that detrended fluctuation analysis (Alados and Huffman 2000; MacIntosh et al. 2011) and the rate of behavioural switching (Ghai et al. 2015) measure different aspects of behaviour, direct comparison between previous results and ours is difficult. However, our study shows that polyparasitism may be an important and more realistic consideration in the assessment of behavioural predictability or behaviour switching, particular given that an unpredictable behaviour is thought to be biologically adaptive (Goldberger 1997; MacIntosh et al. 2011).

Although we found that parasite infections were associated with both activity budgets and behavioural structure, the primary drivers of behavioural change were shifts in food availability; changes in both activity budget and behavioural structure were strongly linked to this. Previous work in our population has identified complex relationships between behaviour and environmental conditions, with food resources, temperature, rainfall and standing water availability strongly influencing activity budgets and mortality (McFarland et al. 2014; Young et al. 2019). Our findings here augment this previous work, providing the first evidence that food availability also affects behavioural structure: behavioural predictability decreased markedly when food availability was higher. This change likely resulted from a trade-off between a decrease in time spent foraging and an increase in both moving and resting when food availability was high. Changes in aspects of behavioural predictability have been shown to have short- and long-term consequences on fitness and survival. These include the success of predator performance in predator–prey interactions where unpredictable prey are more likely to be predated on by aggressive predators (Chang et al. 2017) and mating success, where being a consistent individual does not correlate with mating success (Jennings et al. 2013). However, beyond knowing that behavioural structure can serve as proxy measure of health (Alados and Huffman 2000), the implications for non-human primates are not yet well understood. Here, the use of entropy rate, rather than existing binary approaches, should allow us to identify the consequences of more complex behavioural trade-offs.

Sickness behaviour is increasingly being viewed as an adaptive response to infection (reviewed in Hart 1988; Aubert 1999; Johnson 2002); however, relatively little is known about the consequences of sickness behaviour in social groups. Based on the idea of cytokine-induced sickness behaviour, Hart (1988) proposed that sickness behaviour is an adaptive response to reduce energy consumption when there is a high-energy demand that is necessary to maintain a fever. There was early support for the concept of adaptive behaviour where rats repeatedly chose inactivity over exercise when injected with endotoxin, an endotoxin known to produce an immune response which suggested that that they were motivated to rest (Miller 1964). However, while sickness behaviour may aid in coping with infection, there can be corresponding negative consequences. For example, in the same study population, McFarland (2021) found that monkeys who were febrile and exhibiting sickness behaviour were twice as likely to receive aggression and 6 times more likely to be injured than afebrile monkeys. This suggests that, in social groups, sickness behaviour may incur significant fitness costs. More work is required to fully examine how sickness behaviour may influence the long-term fitness of gregarious mammals.

Taken together, our results provide the foundation for further research on both polyparasitism and the more fine-grained influences of non-lethal parasite infections on behaviour. We suggest that considering multiple parasite infections provides a new perspective on how parasitism shapes behaviour and that further investigation in other populations or with other parasite genera could deepen our knowledge of sickness behaviour in the wild. We also highlight the importance of using a detailed, comprehensive dataset when investigating how environment, physiology and parasitism interact to shape behaviour. In sum, our findings provide additional insight into how animals living in a harsh environment, with strong activity budget constraints, may adopt alternative approaches to parasite infection, avoidance and transmission reduction.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-03111-3.

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Author contribution RB, SPH and LB conceived the ideas and designed the methodology. RB and CY collected the data, and RB, AG and TRB analysed the data. RB, SPH and LB led the writing of the manuscript. All the authors gave approval for publication.

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Data availability Data and scripts are available on Zenodo: 10.5281/zenodo.5199490.

Declarations

Ethics approval All data collection protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505). The Tompkins family, owners of the Samara Private Game Reserve, granted permission to conduct the study on their property in South Africa and also approved the study.

Competing interests The authors declare no competing interests.

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