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Complexity in behavioural organization and strongylid infection among wild chimpanzees

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Objectively measuring the effects of parasitism on animal health is challenging, especially in the wild. Analyses of behavioural organization are increasingly used for this purpose, to identify animals in pathological or otherwise challenged states. Here, we investigated the possible impact of gastrointestinal helminth infection on the behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*, by applying fractal analysis to their feeding patterns. We predicted that higher intensity of strongylid infection should be associated with altered organizational complexity in temporal sequences of behaviour. We observed 15 habituated male chimpanzees in Kalinzu Reserve Forest, Uganda, and collected behavioural time series via focal animal sampling. We quantified the number of strongylid eggs per gram of faecal sediment using a modified simple sedimentation method to estimate the intensity of infection with strongylid nematodes. We used detrended fluctuation analysis (DFA) to explore long-range dependence in binary sequences of feeding behaviour as an index of organizational complexity along a stochastic-deterministic gradient. We then built several generalized linear mixed models to examine the relationship between behavioural organization and strongylid infection. Our results indicate that chimpanzee feeding sequences are long-range dependent and antipersistent, i.e. short bouts tended to be followed by long bouts and vice versa. Furthermore, the complexity of chimpanzee feeding sequences and the intensity of infection with strongylid nematodes were positively related: individuals with more intense infections exhibited more stochastic feeding sequences. In contrast, more conventional analyses did not reveal any relationship between parasitism and chimpanzee behaviour, nor did a survival analysis find variation in the probability of switching between behaviour states across chimpanzees with varying infection phenotypes. This work suggests that strongylid nematodes do pose a challenge for wild chimpanzees, manifest as altered organizational complexity in behaviour sequences, and provides further evidence that fractal analyses can have a valuable role in animal health monitoring.

Habitat degradation, disturbance by anthropogenic activities and increased contact between human and wildlife result in alarming declines in animal populations worldwide (Butchart et al., 2010; Dirzo et al., 2014). It is thus of paramount importance to develop noninvasive methods of monitoring animal health with minimal disruption to wild fauna. Behavioural health monitoring has become a favoured approach in the assessment of the condition of animals because it can be conducted from a distance without requiring any capture or handling of them (Dawkins, 2004; Weary, Huzzey, & Von Keyserlingk, 2009). Advanced analytical tools have been increasingly used to examine structural aspects of animal behaviour sequences, and have the potential to quantify subtly abnormal behavioural patterns in relation to stress and disease (Asher et al., 2009; MacIntosh, 2014; Rutherford, Haskell, Glasbey, Jones, & Lawrence, 2004). These novel methods can be especially

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important for objectively detecting health impairments when no overt clinical signs are induced by infection or other acute or chronic stressors, and there is now major interest in applying such methods more widely to a variety of systems and situations.

Temporal analyses of behavioural organization are particularly promising, as they can reveal added information beyond that found using more traditional approaches based on measures of the frequencies or durations of specific behaviours (Alados, Escos, & Emlen, 1996; Kembro, Marin, Zygadlo, & Gleiser, 2009; Rutherford, Haskell, Glasbey, Jones, & Lawrence, 2003). For example, fractal analysis provides an emerging noninvasive diagnostic tool which enables practitioners to measure the spatial or temporal complexity of a system, i.e. its degree of variability or irregularity in space or over time. Fractal-like structures exhibit patterns that repeat themselves regardless of the scale used to measure them. They are ubiquitous in nature, not only in the physical world in the shape of clouds, trees, mountains and coastlines (Mandelbrot, 1967, 1983), but also in various biochemical and physiological systems, from heart-beat fluctuations to respiratory rates and neuronal networks (Goldberger, Rigney, & West, 1990; Ivanov et al., 1999; Peng, Havlin, Stanley, & Goldberger, 1995). The emergence of fractal structure in biological systems is thought to occur because fractal systems are more ‘error tolerant’, providing better stability and adaptability to cope with rapid external or internal perturbations (MacIntosh, 2014, 2015; West, 1990). In line with this hypothesis, many studies applying fractal analysis to diverse biological systems have demonstrated a loss in complexity in systems operating in pathological states (e.g. Escós, Alados, & Emlen, 1995; Goldberger, 1997; Hausdorff et al., 1997; Goldberger, Amaral et al., 2002; Goldberger, Peng, & Lipsitz, 2002). Such findings highlight the potential power of this method as a diagnostic tool, leading to increased interest in its application, notably in biomedical research (Baish & Jain, 2000; Cross & Cotton 1992; Goldberger, 1996; Varela, Ruiz-Esteban, & De Juan, 2010) but also in the monitoring of animal behaviour (Asher et al., 2009; Kembro, Flesia, Gleiser, Perillo, & Marin, 2013; MacIntosh, 2014; Rutherford et al., 2003). To date, fractal analyses have effectively detected condition-dependent alterations in behavioural organization in a variety of contexts, from toxicological experiments (Alados & Weber, 1999; Kembro et al., 2009; Motohashi, Miyazaki, & Takano, 1993) to production settings (Maria, Escós, & Alados, 2004; Rutherford, Haskell, Glasbey, & Lawrence, 2006) to contexts more relevant to monitoring wildlife (Alados et al., 1996; Cottin et al., 2014; Cribb & Seuront, 2016; MacIntosh, Alados, & Huffman, 2011; Seuront & Cribb, 2011).

This phenomenon, in which the structural organization of behaviour changes in response to a stressor or stressors, is now known as ‘complexity loss’. It rests on the assumption that an optimal configuration in behavioural organization exists (MacIntosh, 2014). In the present study, we used fractal analysis to determine whether the temporal organization along a stochastic-deterministic gradient of behavioural sequences of wild chimpanzees, *Pan troglodytes schweinfurthii*, from Kalinzu Forest Reserve, Uganda, differed in relation to their strongylid parasite infection. Prevalence of gastrointestinal strongylid nematodes is high in wild great apes (Ashford, Reid, & Wrangham, 2000; Krief et al., 2005; Terio et al., 2016), but symptoms of infection are typically absent or at least generally difficult to observe. In general, gastrointestinal nematode infection can impose high energetic costs on hosts (Colditz, 2008), which may induce an overall reduction in their activity levels and alter their normal behavioural patterns (e.g. Ghai, Fugere, Chapman, Goldberg, & Davies, 2015; MacIntosh et al., 2011). Since feeding is among the most fundamental of behaviour states across taxa, we focused on this behaviour in our study, using continuous alternations between feeding and nonfeeding bouts in our analysis.

Overall, we aimed to shed light on the potential impacts of strongylid infection on habituated male chimpanzees using a relatively novel tool. We predicted that higher estimated intensity of strongylid infection should be associated with altered complexity signatures. More specifically, assuming that strongylid infection might pose a chronic rather than acute stressor, it being more or less ubiquitous in the population, we predicted that infection would be associated with reduced organizational complexity, i.e. a more deterministic pattern, in feeding behaviour (Rutherford et al., 2004). We supplemented our study by investigating the possible influence of infection on the rate of behaviour change, following Ghai et al. (2015) who found such effects of whipworm (genus *Trichuris*) infection in red colobus monkeys, *Procolobus rufomitratus tephrosceles*. Finally, more conventional analyses of behaviour were also used to compare with the results obtained via fractal analysis.

METHODS

Study Site and Data Collection

The study was conducted in the Kalinzu Forest Reserve located in the western region of Uganda (0°17′S, 30°07′E, 0°17′E), which covers an area of 137 km^2 (Hashimoto, Furuichi, & Tashiro, 2001). Kalinzu has two rainy seasons in March–May and September–December, with an average annual rainfall of 1584 mm. This study site is situated at altitudes of 1200–1500 m above sea level. Temperatures vary from approximately 15 °C–28 °C throughout the year (Furuichi, Hashimoto, & Tashiro, 2001; Hashimoto, 1995). Vegetation is classified as medium-altitude moist evergreen forest, with common species including *Musanga leo-errerae* and various *Ficus* spp. (Hashimoto, Furuichi, & Tashiro, 1999; Howard, Butler, & Howard, 1991). The forest area is surrounded by savannah, agricultural fields and tea plantations (Yasuoka, Kimura, Hashimoto, & Furuichi, 2012), and it provides habitat for an estimated population of 230 chimpanzees living at a density of 1.55 per km^2. A group named M-group was habituated to human observers in, and has been followed since, 1997 (Hashimoto, 1998; Plumptre, Nampindo, Mutungire, Gonya, & Akuguzibwe, 2008).

Data were collected from March to July 2014. During the current study period, the size of M-group was 97 individuals, including 14 adult males, six adolescent males, 24 adult females and three adolescent females. Because female subjects were difficult to observe on a regular basis, owing to the tendency of chimpanzee females to range alone or in small parties (Hashimoto & Furuichi, 2015), only males were chosen for this study. Data were collected on 15 individuals (Appendix Table A1) whose physical characteristics enabled identification. Among them, five were classed as ‘adolescents’ and four adults were considered as ‘old’ individuals based on their appearance and the time they were first observed in Kalinzu. Subjects were selected for focal follows opportunistically to avoid gaps in potential data collection periods that are introduced when searching for randomly predetermined subjects, but we avoided repeatedly sampling individuals on the same day. We used focal animal sampling (Altmann, 1974) and electronically recorded with a 1 s time resolution whether a focal animal was feeding, foraging, moving, resting or engaging in social behaviour, using CyberTracker 3.317 software (CyberTracker, Cape Town, South Africa). Feeding was defined as the direct consumption of food and foraging as the active acquisition of food items (i.e. searching, handling, extracting food sources). Travelling was recorded when the subject was moving between locations, but excludes displacement while searching for food. Any active or passive interaction between individuals was recorded as social behaviour. Resting was defined as any period in which neither