Health consequences of group living in wild Verreaux's sifakas (*Propithecus verreauxi*)

Dissertation

for the award of the degree

"Doctor rerum naturalium" (Dr. rer. nat.)

of the Georg-August-Universität Göttingen

within the doctoral program Behaviour and Cognition (BeCog)

of the Georg-August University School of Science (GAUSS)

submitted by

Katja Rudolph

from Leipzig, Germany

Göttingen, 2020

Thesis committee

Dr. Claudia Fichtel
Behavioural Ecology and Sociobiology Unit, German Primate Centre, Leibniz Institute for Primate Research, Göttingen

Prof. Dr. Julia Ostner
Behavioural Ecology, Georg-August University, Göttingen & Primate Social Evolution, German Primate Centre, Leibniz Institute for Primate Research, Göttingen

Prof. Dr. Rolf Daniel
Department of Genomic and Applied Microbiology, Georg-August University, Göttingen

Members of the Examination Board

Reviewer: Dr. Claudia Fichtel

Second reviewer: Prof. Dr. Julia Ostner

Further members of the Examination Board

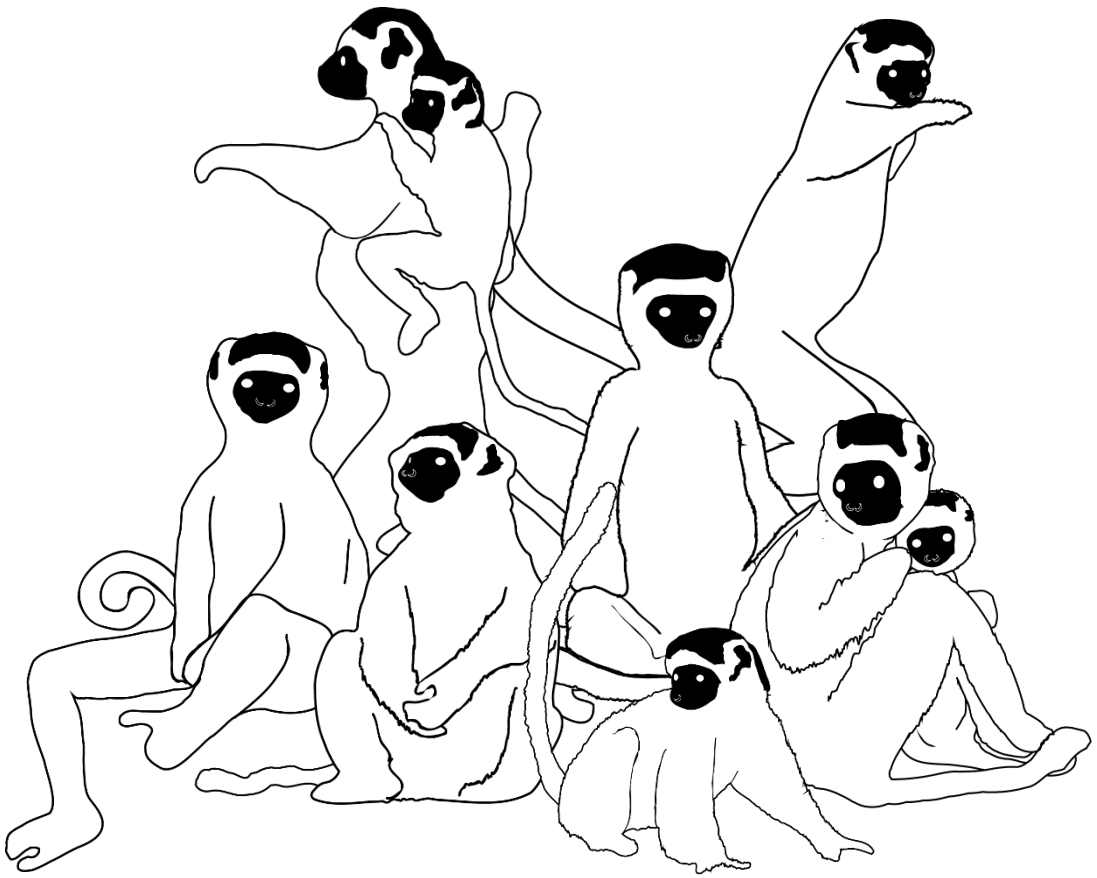
Prof. Dr. Peter M. Kappeler
Behavioural Ecology and Sociobiology Unit, German Primate Centre, Leibniz Institute for Primate Research, Göttingen

Prof. Dr. Rolf Daniel
Department of Genomic and Applied Microbiology, Georg-August University, Göttingen

Prof. Dr. Lars Penke
Biological Personality Psychology Georg-August University, Göttingen

Dr. Dietmar Zinner
Cognitive Ethology Laboratory, German Primate Centre, Leibniz Institute for Primate Research, Göttingen

Date of oral examination: 7th of February 2020



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Summary

The evolution of sociality exposed individuals to several new health-related costs and benefits, which fundamentally affect their survival and reproductive success. Group living provides better access to food and mates and reduces risks of predation, while it also increases competition over shared resources and facilitates the transmission of pathogens. Whereas the general factors favouring the evolution of group living have been well established, little is known about the underlying mechanisms that link aspects of sociality with health. One reason for this limited understanding is the low number of longitudinal studies that have systematically examined this relationship in wild populations.

Here, I add needed data to this field of research by studying links among sociality and indicators of health in 42 individuals of seven neighbouring groups of a wild lemur population - Verreaux's sifakas (*Propithecus verreauxi*). These diurnal primates live in multi-male multi-female groups, have a mainly folivorous diet and inhabit the dry forests of southern and south-western Madagascar, where they are exposed to pronounced seasonality. I examined various aspects of Verreaux's sifakas' social life, i.e. group size, group membership, rank, affiliative and agonistic interactions, and their potential associations with activity and ranging patterns, parasite infections, measures of faecal glucocorticoid metabolites (fGCMs) and gut microbial communities collected over a study period of two consecutive years.

No individual showed signs of sickness and I found only few implications for health-related consequences of sociality in this species. More precisely, group size and social interactions had no impact on behavioural or physiological health-parameters. Between-group variation in activity and ranging patterns likely reflected adaptations to differences in microhabitat features and could be compensated without inflicting changes in fGCMs or parasite infections, i.e. health-related costs. Proximity to group members facilitated the transmission of microorganisms, indicating that gregariousness in this species may indeed come with the cost of parasite transmission, whereas the exchange of beneficial gut microbiota might improve individual health. The results of my thesis imply that health-related consequences of different aspects of group living in Verreaux's sifakas are limited to the effects caused by social proximity but not social interactions.

In conclusion, the magnitude of health consequences of sociality depends on species-specific aspects of their social systems. For example, highly competitive societies with higher rates of agonistic and affiliative interactions among individuals may increase variation in energetic and social stress and facilitate opportunities for transmission of microorganisms. On the contrary, in species with less competitive regimes and low interaction rates, like Verreaux's sifakas, health-consequences of sociality might be attenuated. More comprehensive wildlife studies conducted on species with different social systems and within an ecologically meaningful context are required to improve our understanding of the complex and interrelated factors that contribute to the sociality-health link.

Zusammenfassung

Die Evolution des Soziallebens brachte mehrere neue vor- und nachteilige Konsequenzen für die Gesundheit von Individuen mit sich, welche wesentlichen Einfluss auf deren Überleben und Reproduktionserfolg haben. Das Leben in Gruppen ermöglicht besseren Zugang zu Nahrung und Fortpflanzungspartnern und vermindert das Prädationsrisiko, erhöht aber den Wettstreit um geteilte Ressourcen und vereinfacht die Übertragung von Pathogenen. Während die Faktoren, welche die Evolution des Gruppenlebens begünstigt haben, fest etabliert sind, bleibt das Wissen über die Mechanismen, die dem Zusammenhang von Sozialität und Gesundheit zu Grunde liegen, gering. Ein Grund für dieses begrenzte Verständnis liegt in der bisher geringen Zahl an Langzeitstudien, die den Zusammenhang von Sozialität und Gesundheit systematisch in Wildpopulationen untersucht haben.

Die Erkenntnisse der hier durchgeführten Studie tragen zur Erweiterung des Forschungsfeldes bei, indem Zusammenhänge zwischen Sozialität und Gesundheitsindikatoren bei 42 Tieren aus sieben benachbarten Gruppen einer wildlebenden Population von Lemuren untersucht werden - Verreaux's Larvensifakas (*Propithecus verreauxi*). Diese tagaktiven Primaten leben in Gruppen bestehend aus mehreren Männchen und Weibchen, ernähren sich von vorwiegend von Blättern und bewohnen die Trockenwälder im Süden und Südwesten Madagaskars, wo sie jährlich einem ausgeprägten Wechsel zwischen Regen- und Trockenzeit ausgesetzt sind. Über einen Zeitraum von zwei Jahren, wurden verschiedene Aspekte des Soziallebens der Tiere, d. h. Gruppengröße und -zugehörigkeit, Rang, freundliche und agonistische Interaktionen, und potenzielle Assoziationen mit Aktivitätsmustern, Wanderverhalten, Parasitenbefall, der mikrobiellen Darmflora und Konzentrationen von fäkalen Glucocorticoid-Metaboliten (fGCMs) untersucht.

Keines der Tiere zeigte Anzeichen einer Erkrankung und es gab nur wenige Hinweise darauf, dass das Sozialleben der Spezies Auswirkungen auf die Gesundheit der Individuen hat. Genauer gesagt hatten Gruppengröße und soziale Interaktionen keinen Einfluss auf Verhaltens- oder physiologische Parameter. Variationen in Aktivitätsmustern und Wanderverhalten zwischen den Gruppen reflektierten vermutlich Anpassungen an Unterschiede in den Mikrohabitaten, sorgten aber nicht für Veränderungen in fGCMs oder Parasitenbefall, was darauf hinweist, dass diese Anpassungen keine gesundheitlichen Auswirkungen hatten. Die Nähe zu Gruppenmitgliedern vereinfachte die Übertragung von Mikroorganismen, was darauf schließen lässt, dass das Leben in Gruppen in Bezug auf Parasitenübertragungen nachteilig sein kann, wohingegen der Austausch nutzbringender Darmbakterien gesundheitsfördernde Auswirkungen haben könnte. Die Ergebnisse dieser Dissertation implizieren, dass verschiedene Aspekte des Gruppenlebens in Verreaux's Larvensifakas eingeschränkte Konsequenzen für die Gesundheit der Tiere haben, welche durch soziale Nähe, nicht aber durch soziale Interaktionen verursacht werden.

Schlussendlich hängt das Ausmaß der gesundheitsbezogenen Konsequenzen von Sozialität von den artspezifischen Aspekten des jeweiligen Sozialsystems ab. In Arten mit hoch-kompetitiven Sozialgefügen und höheren Raten an agonistischen und freundlichen Interaktionen zwischen Individuen, könnte es beispielsweise zu größeren Variationen in energetischem und sozialem Stress kommen und Möglichkeiten der Übertragung von Mikroorganismen könnten zunehmen. Im Gegensatz dazu wären die gesundheitsbezogenen Konsequenzen von Sozialität in Arten mit weniger kompetitiven Regimen und niedrigeren Interaktionsraten, wie es zum Beispiel bei Verreaux's Larvensifakas der Fall ist, vermindert. Zur Anknüpfung an diese Thematik sind weitere Freilandstudien mit verschiedenen Sozialsystemen im ökologisch relevanten Kontext nötig, um eine Verständniserweiterung der komplexen und voneinander abhängigen Faktoren zum Zusammenhang von Sozialität und Gesundheit zu ermöglichen.

Chapter 1

General Introduction

1.1 Towards Understanding the Evolution of Sociality

When, how and why did animals begin to live in groups? Why do some species form larger groups than others? What are the trade-offs of being social? The evolutionary switch from solitary to group living represents one of the major transitions in evolution as it had fundamental consequences for animals' life histories (Szathmáry and Smith, 1995). A better understanding of the basic principles and consequences of this transition yields novel practical applications for various scientific disciplines, like immunology, neurology, genetics, ecology or computer science, and will shed more light on the history and evolution of humans' complex societies. However, despite the great deal of scientific progress that has been made in recent years, there remain many questions surrounding the evolution of sociality to be answered.

The Troublesome Semantics

Even though the mechanisms and factors that governed the transition from solitary to group living have been studied in depth (Krause and Ruxton, 2002; Ward and Webster, 2016), research still struggles to amend a unified conceptual framework applicable to all disciplines and taxa. This is partly due to the missing consent on the use of semantics (Costa and Fitzgerald, 2005, 1996; Krause and Ruxton, 2002). For example, there is disagreement on the definition and use of the term "social". Some researchers refer to animals as social if their range of behaviours involves interactions with conspecifics (Brown, 1975), while others speak of an interdependence of conspecifics that forage together and thereby affect each other's energetic gains and losses (Giraldeau and Caraco, 2018). To make things more complicated, there is an increasing amount of vertebrate literature assigning degrees of sociality to certain species by using terms like "highly social" or "socially complex" without providing explicit definitions (Kappeler et al., 2015). Meanwhile, studies of invertebrates apply categories to sociality, e.g. "semi-social", "parasocial" or "quasi-social", which cannot be easily applied to vertebrates (Costa and Fitzgerald, 2005). Throughout this thesis, I will apply the term "social" in the sense of Tinbergen's definition: "An animal is called social when it strives to be in the neighbourhood of fellow members of its species when performing some, or all, of its instinctive activities" (Tinbergen, 1951).

Following on from this, there also exist numerous definitions for the terms "group" and "social group" (see Krause and Ruxton, 2002; Ward and Webster, 2016). The difficulty lies in finding definitions that applies to all species. For example, some animals form short-term aggregations in response to temporally or spatially clumped resources, while others may live permanently in close proximity to conspecifics. Here, I consider a species as group living, if two or more conspecifics spent a significant

amount of time in proximity close enough to allow continuous information exchange (modified from Pitcher (1983)). I refer to species as living in social groups, if they additionally interact with their group members "to a distinctly greater degree than with other conspecifics" (Struhsaker, 1969; Wilson, 1975).

Why Become Social?

The majority of animal species live solitary, which is considered the ancestral condition of animals' social systems (Lukas and Clutton-Brock, 2013; Majolo and Huang, 2018). Permanent co-residency with conspecifics elicits competition for resources and mates and stable aggregations of animals only occur if competition among individuals can be overcome by the benefits of gregariousness (Krause and Ruxton, 2002; Ward and Webster, 2016). Such benefits are generally related to predation risks, access to food and access to mating opportunities (Alexander, 1974; Hamilton, 1971; van Schaik et al., 1983). Taxa in which benefits of gregariousness outweighed its costs, eventually formed groups of different sizes, compositions and stability, leading to the emergence of a wide array of diverse social systems ranging from small pair-bonded units to large aggregations (Ward and Webster, 2016). However, there remains little knowledge about the consequences of group living and how these consequences may vary across social systems or individuals within the same group (Kappeler et al., 2015; Silk, 2007).

Health-Related Costs and Benefits of Sociality

There is accumulating evidence on a wide range of taxa linking aspects of sociality to differential survival and reproductive success (Archie et al., 2014; Bilde et al., 2007; Cameron et al., 2009; House et al., 1988; Jungwirth and Taborsky, 2015; Meunier, 2015; Oli and Armitage, 2003; Ostner and Schülke, 2018; Silk, 2007; Verbrugge, 1979). For example, humans with stronger social relationships live longer (Holt-Lunstad et al., 2010), horses, baboons and dolphins that are better socially integrated benefit from higher birth rates and offspring survival (Cameron et al., 2009; Frère et al., 2010; McFarland et al., 2017; Silk et al., 2003), and colony size in social spiders is positively linked to offspring survival but decreases individual reproductive success (Avilés and Tufiño, 1998). While the link between sociality and fitness is well established and reproducible, the behavioural and physiological mechanisms by which these links are exerted remain not well understood. One mediator for the fitness consequences of sociality is individual health (Kappeler et al., 2015), which can be both, improved or worsened by different aspects of group living.

Defining "Health"

To understand and compare health consequences of sociality, it is necessary to first find a broad agreement on how to define health. This has, however, proven difficult in the past and debates have been ongoing for centuries, resulting in numerous proposals (Chatfield, 2018; van de Belt et al., 2010). The most accepted and commonly used definition was provided by the WHO (World Health Organisation),

which defines health as "a state of complete physical, mental and social wellbeing and not merely the absence of disease or infirmity" (World Health Organization, 1948). However, this definition has received much criticism due to its static nature, i.e. health as a state, and its requirement for completeness, which would be hardly ever fulfilled by anyone (Jambroes et al., 2016; Smith, 2008). Other objections concerning changes in disease patterns and societies' demography within the last 50 years or discrepancies between the terms "health" and "wellbeing" were brought up (reviewed in Chatfield, 2018; Huber et al., 2011). A new proposal for conceptualising health was presented in 2011, defining health as "the ability to adapt and to self-manage' when facing physical, mental, and social challenges" (Huber et al., 2011). Accordingly, health is considered more dynamic as it describes individuals' capacities of maintaining physiological homeostasis. This way health can be evaluated with a set of dynamic and interrelated features, which offer valuable information about various aspects of individual condition. It is therefore that I will apply the term "health" in the sense of this definition.

Parasites and Diseases

One of the major health-related costs of group living constitutes the transmission and spread of parasites and diseases (Alexander, 1974; Freeland, 1976). Parasites can be transmitted via two pathways: directly, e.g. through physical contact, or indirectly, e.g. through shared environments (White et al., 2017). Physical contact to conspecifics presumably increases opportunities for direct transmissions, which is why transmission rates are generally expected to increase with group size or group density (Altizer et al., 2003; Nunn et al., 2003; but see Rifkin et al., 2012). Characteristics of species' social networks can provide more information about groups' structures and animals' social relationships (Wey et al., 2008) and potentially enable a better understanding of transmission dynamics than measures of group size (Poulin, 2018). For example, in female Japanese macaques (*Macaca fuscata yakui*) central position within groups was correlated with increased nematode infections (MacIntosh et al., 2012), and type and direction of physical contacts explained helminth prevalence in brown spider monkeys (*Ateles hybridus*) (Rimbach et al., 2015) and the spread of infectious fungi in garden ant colonies (*Lasius neglectus*) (Theis et al., 2015). Infestation with environmental parasites might be facilitated if increased host density leads to higher environmental contamination and, therefore, increased contact with infectious parasite stages (Chapman et al., 2005; Ezenwa, 2004; Poirotte et al., 2016). The transmission of sexually transmitted diseases is expected to increase with promiscuity, constituting another example for the exploitation of host social behaviour through pathogens (Nunn et al., 2014; Thrall et al., 2000).

Group living animals also embark strategies to defend themselves against parasites and diseases (Schmid-Hempel, 2017). For example, allogrooming in primates can reduce ectoparasite load (Akinyi et al., 2013; Duboscq et al., 2016; Nunn and Altizer, 2006; Sánchez-Villagra et al., 1998). In garden ants, grooming of individuals with fungal infections can be mutually beneficial as the groomee gets alleviated

from the infection, while the groomer receives a low-level fungal infection, promoting immunisation (Konrad et al., 2012). This "social immunisation" (Cremer et al., 2007; Konrad et al., 2012; Traniello et al., 2002) has also been observed in vertebrates, where low-level exposures to pathogens through proximity to conspecifics lead to the development of adaptive immunity (Hart, 2011).

Immune System Functionality

The immune system provides a powerful defence against parasites and diseases that functions via multiple pathways but comes with high energetic costs (Sheldon and Verhulst, 1996; Straub et al., 2010). Individuals living in groups frequently compete over food and mates, which can impose energetic constraints, especially to those with inferior competitive abilities (Lane et al., 2010; Metcalfe, 1986; van Schaik et al., 1983). If energetic constraints persist, individuals might not be able to allocate sufficient energy to their immune system, resulting in reduced immunocompetence and increased susceptibility to infectious agents (Kappeler et al., 2015). For example, specific ranks within social hierarchies can impose varying energetic requirements to individuals (Emery Thompson et al., 2010). This might explain why rank-related differences in health are partly associated with rank-related differences in immune system functionality (Fairbanks and Hawley, 2012; Habig et al., 2018; Habig and Archie, 2015; Snyder-Mackler et al., 2016). Social stress can also impair immune functions, as negative life events and social isolation in humans, and increased social conflict in animals are associated with increased vulnerability to diseases (Cohen et al., 2012, 1997; Holt-Lunstad et al., 2010; McEwen, 2012; McEwen et al., 1997; Widom, 1999).

Stress and Glucocorticoids

Links between social stress and individual's immune responses are presumably mediated via the activities of the hypothalamic–pituitary–adrenocortical (HPA) system, which releases glucocorticoids (GCs) – one of the most studied adrenal hormones (Creel et al., 2013; Defolie et al., 2019; Goymann and Wingfield, 2004; Sapolsky et al., 2000). GCs' main function lies in energy balance modulation, but they are also involved in a myriad of other physiological processes, including their role within the body's complex physiological stress response (Beehner and Bergman, 2017; Higham, 2016). GCs get released into the body within minutes to hours after an acute stressor triggered the activation of the HPA axis (Sapolsky et al., 2000) and can impact behaviour and metabolic, reproductive, and immune systems (Landys et al., 2006; Romero et al., 2009; Sapolsky et al., 2000). Their effects can be both, immunoenhancing and immunosuppressive, e.g. through regulation of inflammatory processes (Besedovsky et al., 1986; Dhabhar, 2009; Elenkov and Chrousos, 1999) or by triggering changes in blood leukocyte distributions (Dhabhar et al., 1996; Fauci and Dale, 1974). Some studies found associations between increased concentrations of GCs and slower rates of wound healing (Archie et al., 2012; French et al., 2006; Walburn et al.; but see 2009 Archie, 2013).

Due to their impact on immune functions, their ubiquity across vertebrates and multiple non-invasive sampling possibilities (e.g. via faeces, urine, saliva), studies in stress biology rely more and more on GC measures as biomarkers for stress (McCormick and Romero, 2017). However, in the first place, GCs are metabolic hormones that provide energy to the body when required and reflect energetically demanding periods, e.g. during different reproductive stages or circannual variation in temperatures and food availability (Beehner and Bergman, 2017). An increase in GCs is, therefore, not necessarily associated with a stress response, which is why GC concentrations do not constitute reliable indicators of individual stress levels (Beehner and Bergman, 2017; Higham, 2016; MacDougall-Shackleton et al., 2019). Nevertheless, measures of GCs allow researchers to measure the energetic costs of sociality, which is why they provide a valuable resource for understanding the sociality-health nexus.

In numerous studies, different aspects of group living have been linked to variation in GC concentrations (reviewed in Creel et al., 2013; Raulo and Dantzer, 2018). For example, in mammals, measures of GCs were positively correlated to population density or group size (Boonstra and Boag, 1992; Dantzer et al., 2013; Foley et al., 2001; Raouf et al., 2006). Differences in social status can be accompanied by varying energetic constraints and, thus, changes in GC concentrations (Abbott et al., 2003; Emery Thompson et al., 2010; Gesquiere et al., 2011). However, whether higher or lower ranks are energetically more costly and trigger GC secretion depends on different aspects of a species social system, like social structure, social organisation or mating system (Beehner and Bergman, 2017; Sapolsky, 2005). Moreover, agonistic interactions, social isolation and social instability (Cavigelli et al., 2003; Culbert et al., 2018; Dantzer et al., 2017; Girard-Buttoz et al., 2009; van Meter et al., 2009) are often linked to increased GC outputs, while opposite effects are reported for affiliative interactions (Raulo and Dantzer, 2018).

GCs exert powerful effects on animals' behaviours and physiology, and links between GC concentrations and social behaviours are well established. However, there exist a variety of intrinsic and extrinsic factors that can trigger and modulate GC secretions and ought to be controlled for in endocrinological research (Higham, 2016; Rimbach et al., 2013). One of these confounding factors is the gut microbiome (Foster et al., 2017).

Bacterial Gut Microbiota

Humans and animals harbour trillions of bacteria within their gastrointestinal tracts that play major roles for their health and fitness. Gut bacteria enable digestion, produce vitamins from the diet, they influence immune system development and protect their hosts from infection (Kinross et al., 2011; Ley et al., 2005; Turnbaugh et al., 2006a). Especially within the last decade, a basic understanding of the functions microbial communities have in human health and diseases has been established (Cresci and Bawden, 2015), while their role in other animals has yet to be investigated in depth.

The assemblage of the gut microbiota can be influenced by numerous intrinsic factors, like age (Amato et al., 2014; Pafčo et al., 2019), sex (Dominianni et al., 2015; Ren et al., 2016), or host genotype (Dąbrowska and Witkiewicz, 2016; Degnan et al., 2012a; Kovacs et al., 2011); and extrinsic factors, like parasites (Boutin et al., 2013; Morton et al., 2015) or diet (Greene et al., 2018; Youngblut et al., 2019). Social behaviours can also modify gut microbiome composition and diversity (Ezenwa et al., 2012; Gilbert, 2015; Lombardo, 2008; Montiel-Castro et al., 2013) as shown in various taxa, ranging from insects (Koch and Schmid-Hempel, 2011) and birds (Kulkarni and Heeb, 2007) to carnivores (Theis et al., 2015) and primates (Clayton et al., 2018). Group living animals often share more similar gut microbial communities with group members than with outsiders (Bennett et al., 2016a; Chiyo et al., 2014; Grieneisen et al., 2017; Raulo et al., 2017) and studies in primates found rates of social interactions to covary with gut microbiome similarity (Moeller et al., 2016; Tung et al., 2015).

There are multiple bidirectional connections that link the gut microbiota with its host's central nervous system via endocrine, immune and neural pathways. These connections are summarised in the term "gut-brain axis" (Foster et al., 2017; Grenham et al., 2011; Montiel-Castro et al., 2013). A growing number of studies suggests that gut bacteria play a fundamental role in regulating their host's immune system, physiological stress response and other important physiological functions and, thus, have profound impact on host health. For example, HPA axis reactivity can be influenced through experimental alterations of gut microbial communities (Carabotti et al., 2015; Neufeld et al., 2011; Sudo, 2014) and increases in GC concentrations have been linked to decreased microbial diversity or changes in the abundance of certain microbial phyla in gorillas (*Gorilla gorilla gorilla*) (Vlčková et al., 2018) and yellow-legged gulls (*Larus michahellis*) (Noguera et al., 2018). Similarly, a recent study on grey squirrels (*Sciurus carolinensis*) found links between various measures of HPA activity, including GC metabolites, and gut microbiome composition and diversity (Stothart et al., 2019). Moreover, cases of dysbiosis – an imbalance of the gut microbial community – are associated with lower serum immunoglobulin levels, decreased lymphocytes (Round and Mazmanian, 2009) and various intestinal, metabolic and central nervous system-related disorders (Rinninella et al., 2019).

Various aspects of sociality can benefit individual health via the social transmission of gut bacteria. More precisely, socially transmitted bacteria can contribute to pathogen resistance and stimulate host immunity (Koch and Schmid-Hempel, 2011; Montiel-Castro et al., 2013). Commensal microbes might also outcompete pathogens for resources or produce by-products that inhibit pathogens (Abt and Pamer, 2014; Ezenwa et al., 2016). Moreover, frequent social transmission may increase microbial diversity, which is associated with improved health (Browne et al., 2017).

Altogether, there is increasing evidence that social interactions are associated with health-related trade-offs. However, inter- and intraspecific variability in the patterns that link various health-indicators with various aspects of sociality remains high (Kappeler et al., 2015). One reason for this is that

physiological parameters of health, like parasites, GCs and microbiomes, are highly interrelated and studies that explicitly examine multiple health indicators simultaneously in order to gain a comprehensive understanding of their interactions are still missing. Moreover, most knowledge on the sociality-health nexus is based on clinical and laboratory studies, which is why the understanding of the relative importance, underlying mechanisms, dynamics and interactions of social factors on individual health in wild animal populations is still relatively poor (Gesquiere et al., 2011; Huffman and Chapman, 2009; Nunn and Altizer, 2006; Silk et al., 2010).

The Indispensable Value of Comprehensive Field Research

Within the last decades, laboratory studies enabled major discoveries in and created the fundament for today's parasitological, endocrinological and microbial research. However, studies in artificial environments are unable to replicate the manifold factors animals face under natural conditions, which is why field studies are of great importance when studying links between sociality and health. Various environmental factors can influence animal physiology and behaviours, such as seasonal changes in temperatures and food availability (Bekoff et al., 1984; Bronikowski and Altmann, 1996; Iwamoto and Dunbar, 1983), habitat quality (Franklin et al., 2000; Strandburg-Peshkin et al., 2017), or anthropomorphic disturbances (Junge et al., 2011; Marty et al., 2019; van Meter et al., 2009). Inclusion of potentially confounding factors increases the general understanding of the links between social behaviours and their physiological consequences in wild animals. Moreover, great progress has been made on the application of non-invasive techniques to collect and analyse samples without disturbing animals' natural behaviours. This progress allows studies to gain greater ecological validity and to widen the range of species that can be tested under natural conditions (Higham, 2016).

1.2 Studying Lemurs

Without nonhuman primates (hereafter referred to as primates), humans would be - phylogenetically speaking - isolated from the rest of the animal kingdom and attempts to study human social evolution would be limited to testing theories based on general principles applicable to all mammals. Fortunately, however, there exist over 500 different primate species which show high diversity in social complexity (Mitani et al., 2012). At least 79 % of primate species are group living (Silk and Kappeler, 2017) and the manifold nature of primates' social systems makes them particularly useful for interspecific comparative studies on the evolution of group living and the several new health-and fitness-related costs and benefits that derived from this evolution.

Lemurs represent an especially interesting primate radiation for studies on the evolution of sociality. They are endemic to the island of Madagascar where they evolved from one common ancestor independently from anthropoid primates (Mitani et al., 2012). Lemur groups show three major

differences to their continental relatives. First, they are smaller, most likely because of adaptations to feeding competition (Kappeler and Heymann, 1996; Wright, 1999). Second, they display fairly even sex ratios, which might be explained through their relatively recent evolutionarily transition to group living (Kappeler et al., 2009a; van Schaik and Kappeler, 1996). Third, not all types of social organisations that can be found in anthropoids are represented in lemurs, e.g. there are no groups with single breeding males ("harems") or females ("polyandrous groups") and their groups never comprise multiple social layers as can be found, for example, in baboons (Mitani et al., 2012). Therefore, examinations of consequences of sociality in lemurs will prove useful since they provide new insights into the similarities and dissimilarities of health and fitness consequences of social behaviours between different primate radiations, which will help to explain general principles of the evolution of group living.

Verreaux's Sifakas as Study System

In this thesis, I studied health-consequences of group living in a wild population of Verreaux's sifakas (*Propithecus verreauxi*) at Kirindy Forest, in western Madagascar. There are nine different species within the genus *Propithecus* (family *Indriidae*), which are distributed throughout the whole island (Figure 1). All of them are group living, arboreal and belong to the larger representatives among lemurs (Mittermeier et al., 2008). Verreaux's sifakas are diurnal, have a frugi-folivorous diet, inhabit the dry forests of southern and south-western Madagascar and live in small multi-male multi-female groups ranging in size from 2 to 12 animals (Jolly et al., 1982; Kappeler and Fichtel, 2012; Leimberger and Lewis, 2015; Sussman et al., 2012). This species was one of the first lemurs to be studied in the wild (Jolly, 1966; Richard et al., 2002) and to date much research has been conducted on their social organisation, life histories, mating tactics, and intergroup relations (Benadi et al., 2008; Erkert and Kappeler, 2004; Kappeler and Fichtel, 2012; Koch et al., 2016a; Markham and Gould, 2018; Springer et al., 2016).

Previous work on the population at Kirindy Forest suggests that Verreaux's sifakas are well suited for studying health consequences of sociality because:

1) Measures of faecal glucocorticoid metabolites (Fichtel et al., 2007) and parasitism (Springer and Kappeler, 2016) are well established and validated, and GPS tags have been successfully applied to record long-term ranging patterns (Koch et al., 2016a).

2) With 7 habituated, adjacent groups (Figure 2), the population in Kirindy Forest is at the upper end in terms of study groups compared to field research in other primates (see e.g. Fürtbauer et al., 2014; Ganas and Robbins, 2005; Markham et al., 2015; Snaith and Chapman, 2008; Stevenson and Castellanos, 2000).

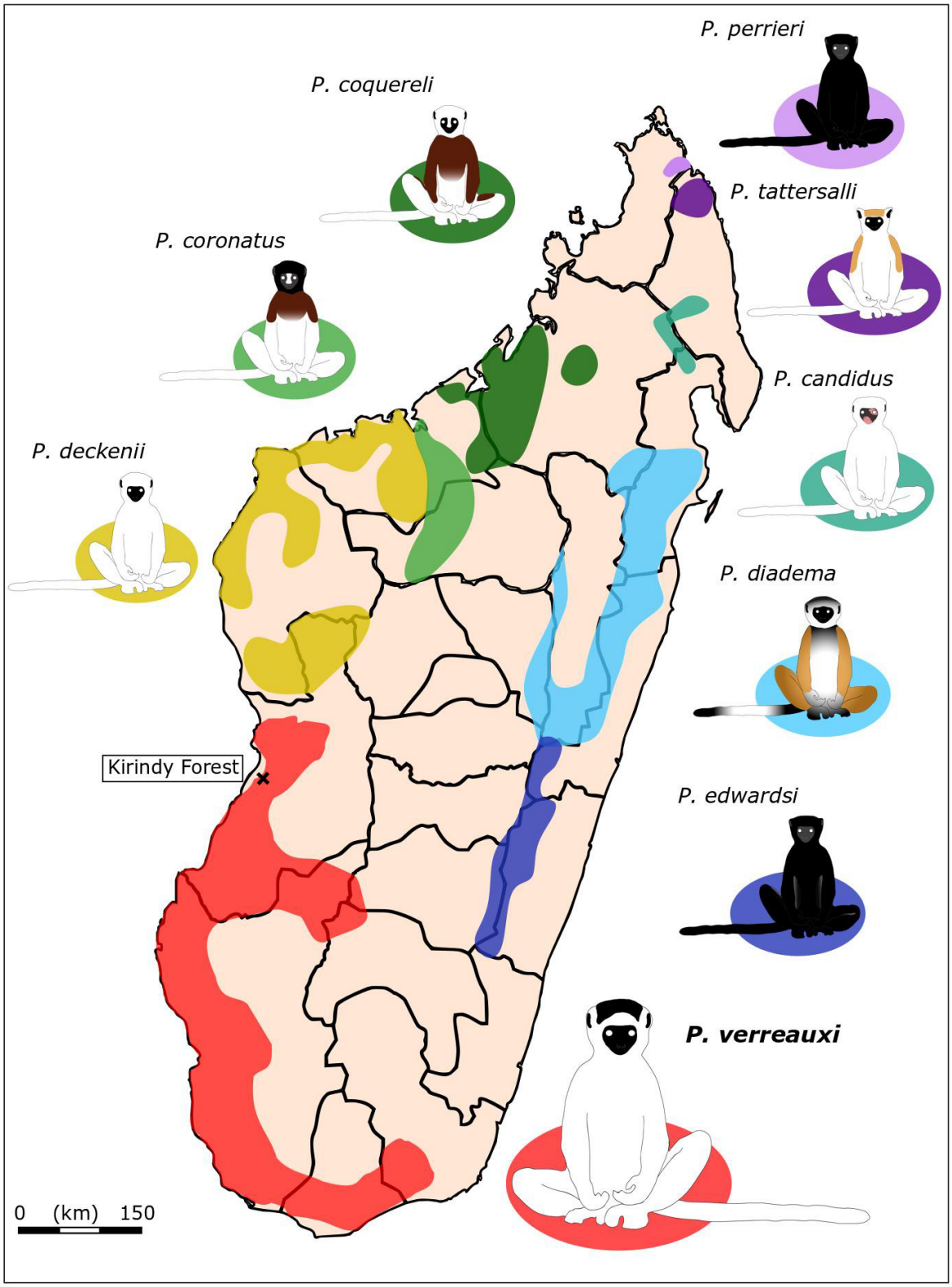


Figure 1 Illustration of the distribution of the nine different Propithecus species (based on www.iucnredlist.org, access date 01/12/2019). The map was created by Vemaps.com and modified by Katja Rudolph

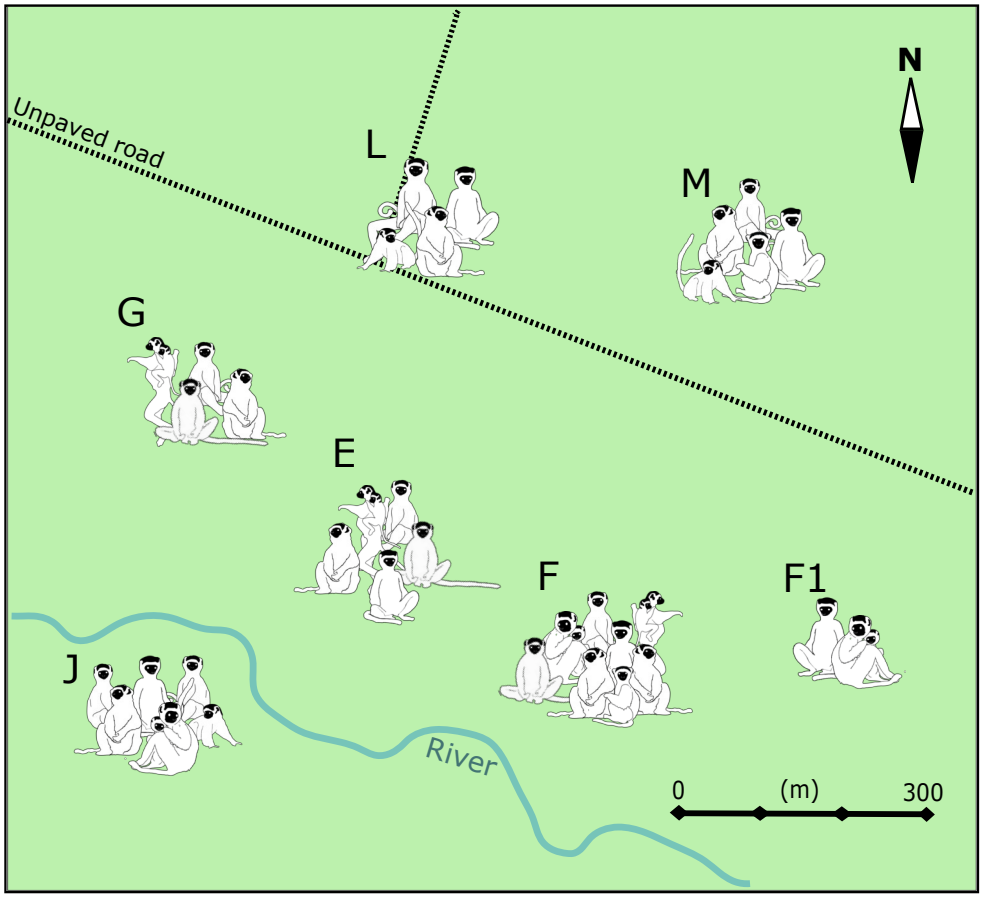


Figure 2 Schedule of the study site with the location of seven study groups at Kirindy Forest, Madagascar. Letters indicate labels of the groups

Figure 3 An adult female Verreaux's sifaka with radio collar

3) Most knowledge that has been gained on the sociality-health nexus in wild primate populations derives from species living in large groups with up to > 50 individuals, e.g. yellow and chacma baboons (*Papio cynocephalus and P. hamadryas ursinus*) (Crockford et al., 2008; Markham et al., 2015; Silk et al., 2010), chimpanzees (*Pan troglodytes*) (Wittig et al., 2016) or Japanese macaques (Duboscq et al., 2016), while species living in smaller groups are underrepresented. However, interspecific variation in health and fitness consequences of group living may crucially depend on group size (Chapman and Chapman, 2000; Wrangham et al., 1993).Investigations of the sociality-health nexus in a lemur species that lives in small groups will, therefore, provide new insights into the impact of group size on health-related consequences of sociality.

Figure 4 Kirindy Forest during the wet (left) and the dry season (right). © Katja Rudolph

4) Kirindy Forest is subject to pronounced seasonality, with a long, cool dry season (April to October) and a hot wet season (November to March) (Kappeler and Fichtel, 2012; Figure 4). Since the study population is part of an ongoing long-term study (Kappeler and Fichtel, 2012), data on monthly precipitation, temperatures and phenology are collected in great detail, allowing to control for various ecological confounding factors.

1.3 Objectives of This Thesis

The general aim of my thesis is to illuminate components and links of the sociality-health nexus in a wild population of Verreaux's sifakas. Therefore, I examine associations of various aspects of sociality within and between groups with an array of behavioural, physiological and ecological variables, some of which function as indicators for animals' physical condition. Over two consecutive years and with the help of

field assistants, I collected and analysed a comprehensive data set comprising ranging, feeding and social behaviours and measures of faecal glucocorticoid metabolites (fGCMs), parasites and bacterial gut communities.

In study 1 (chapter II), I test predictions of the *ecological constraints* and the *optimal group size hypothesis*, which link group size to condition and health. I investigate the impact of group size and group membership on daily travel distances, home range sizes, daily activities, fGCMs and parasite richness while controlling for the potentially confounding effects of seasonality and habitat quality.

After examining fGCM concentrations between groups in study 1, I focus in study 2 (chapter III) on fGCM variations between individuals. To better understand the dynamics and determinants of fGCMs, I investigate potential associations with social interactions, group composition, rank, reproductive state, vigilance, scratching, diet, food availability and daily temperature differences - factors that are all suggested to impact GC outputs in vertebrate species.

In study 3 (chapter IV), I investigate the drivers of between-group variation in bacterial gut communities. An increasing number of studies in a wide range of taxa, including Verreaux's sifakas, finds group members to share more similar gut bacterial communities than individuals living in different groups (Grieneisen et al., 2017; Koch and Schmid-Hempel, 2011; Lax et al., 2014; Springer et al., 2017; Theis et al., 2012). However, the drivers of this microbial convergence among group members remain little understood. I combine data on social interactions, maternal relatedness, diet, habitat structure, habitat overlap and seasonality with measures of gut microbial communities, derived from 16S rRNA sequencing, to evaluate the relative contribution of social, genetic and ecological factors to shaping groups' distinct gut microbiomes.

Chapter 2

Study I

One Size Fits All? Relationships Among Group Size, Health, and Ecology Indicate a Lack of an Optimal Group Size in a Wild Lemur Population

with Claudia Fichtel[1,3], Dominik Schneider[4], Michael Heistermann[5], Flávia Koch[1], Rolf Daniel[4], and Peter M. Kappeler[1,2,3]

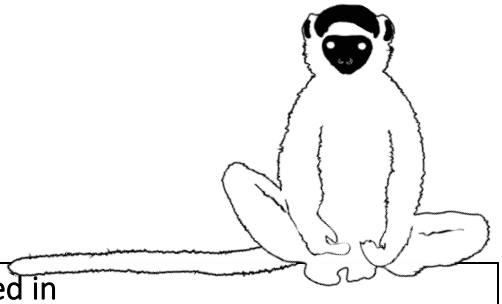
[1] Behavioral Ecology & Sociobiology Unit, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[2] Dept. Sociobiology /Anthropology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology, University Göttingen, Göttingen, Germany

[3] Leibniz Science Campus "Primate Cognition", Göttingen, Germany

[4] Genomic and Applied Microbiology and Göttingen Genomics Laboratory, Institute of Microbiology and Genetics, University Göttingen, Göttingen, Germany

[5] Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany



This chapter is published in

Behavioral Ecologogy and Sociobiology (2019) 73: 132

https://doi.org/10.1007/s00265-019-2746-0

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https://doi.org/10.1007/s00265-019-2746-0

ORIGINAL ARTICLE

One size fits all? Relationships among group size, health, and ecology indicate a lack of an optimal group size in a wild lemur population

Katja Rudolph[1,2,3] · Claudia Fichtel[1,3] · Dominik Schneider[4] · Michael Heistermann[5] · Flávia Koch[1] · Rolf Daniel[4] · Peter M. Kappeler[1,2,3]

Received: 19 April 2019 / Revised: 19 August 2019 / Accepted: 21 August 2019

Abstract

Group size is a key component of sociality and can affect individual health and fitness. However, proximate links explaining this relationship remain poorly understood, partly because previous studies neglected potential confounding effects of ecological factors. Here, we correlated group size with various measures of health while controlling for measures of seasonality and habitat quality, to explore trade-offs related to group living in a mainly folivorous primate—Verreaux's sifakas (*Propithecus verreauxi*). Over a course of 2 years, we studied 42 individuals of 7 differently sized groups (range 2–10) and combined measures of faecal glucocorticoid metabolites ($n > 2300$ samples), parasitism ($n > 500$ samples), ranging and activity patterns, together with estimates of habitat quality (measures of ~ 7000 feeding trees). None of our measures was correlated with group size, while seasonality, but not habitat quality, impacted almost all examined variables. We conclude that group size alone might be insufficient to explain patterns in the sociality-health nexus or that the small range of group sizes in this species does not induce effects suggested for species living in larger groups. An optimal group size balancing the advantages and disadvantages of living in differently sized groups may not exist for Verreaux's sifakas. Our results do not support predictions of the *ecological constraints hypothesis* or the *optimal group size hypothesis* as they may only account for species limited in group size by ecological factors—a condition that may not apply to the majority of folivorous mammals, which seem to be limited by social factors.

Communicated by M. A. van Noordwijk

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-019-2746-0) contains supplementary material, which is available to authorized users.

✉ Katja Rudolph
KRudolph@dpz.eu

Claudia Fichtel
Claudia.fichtel@gwdg.de

Dominik Schneider
dschnei1@gwdg.de

Michael Heistermann
MHeistermann@dpz.eu

Flávia Koch
biokoch@gmail.com

Rolf Daniel
rdaniel@gwdg.de

Peter M. Kappeler
pkappel@gwdg.de

[1] Behavioral Ecology & Sociobiology Unit, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

[2] Department Sociobiology/Anthropology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology, University Göttingen, Kellnerweg 6, 37077 Göttingen, Germany

[3] Leibniz Science Campus "Primate Cognition", Göttingen, Germany

[4] Genomic and Applied Microbiology and Göttingen Genomics Laboratory, Institute of Microbiology and Genetics, University Göttingen, Grisebachstraße 8, 37077 Göttingen, Germany

[5] Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

Published online: 29 August 2019

Significance statement

Group size is a key component of group living and can crucially impact individual health. Ecological variables may modulate this relationship, but they were often neglected in previous studies. To better understand the links between sociality and health, we, for the first time in a mammal, simultaneously examined variation in ranging patterns, daily activities, glucocorticoid concentrations, and parasitism as a function of group size and under consideration of measures of seasonality and habitat quality in wild Verreaux's sifakas (*Propithecus verreauxi*). Group size had no impact on individual health indicators, while seasonal variation in food availability and temperature differences, but not habitat quality, affected the majority of variables. We demonstrate strong impacts of environmental factors on socio-ecological traits and conclude that group size on its own might be insufficient to explain patterns in the sociality-health nexus.

Keywords Optimal group size · Glucocorticoids · Parasites · Daily travel distance · Habitat quality · *Propithecus verreauxi*

Introduction

Group size has been identified as one key aspect of sociality that influences an individuals' condition and health (Altizer et al. 2003; Borries et al. 2008; Markham et al. 2015; Ezenwa et al. 2016). According to the *ecological constraints hypothesis*, feeding competition, parasite infestations, and energy expenditure should be higher in larger groups, whereas smaller groups face higher per capita predation risk and disadvantages during competitive encounters with larger groups (Wrangham et al. 1993; Chapman and Chapman 2000, but see Koch et al. 2016). The *optimal group size hypothesis* posits that intermediate-sized groups represent a balance between the tendency to aggregate to increase predator safety and the tendency for large groups to fission as a consequence of increased food competition (Terborgh and Janson 1986). Thus, in order to optimize the consequences of group size variation, there should be selection for intermediate-sized or "optimal" group size in which individuals carry the lowest costs of group living and, therefore, ought to be healthiest and fittest (Chapman and Chapman 2000). Yet, intra-specific group size variation persists, but the proximate links between group size and health remain poorly understood.

One important link between sociality and health is the physiological stress response. Stressors are uncontrollable stimuli derived from extrinsic and intrinsic sources that trigger a reaction of the vertebrate hypothalamic-pituitary-adrenal (HPA) axis leading to the secretion of glucocorticoids (GCs) (Adkins-Regan 2005; Koolhaas et al. 2011). GCs are mainly responsible for the regulation of metabolic functions (Sapolsky et al. 2000; Beehner and Bergman 2017), in particular, mediating energy homeostasis during energetically demanding periods (Romero et al. 2009) and energetically costly behaviours, like locomotion (Dunn et al. 2013). When individuals enter a state of "stress", a rise of GC secretions initiates various behavioural and physiological changes to cope with the challenge (Busch and Hayward 2009), affecting individuals' immune functions and, therefore, ultimately also their health (Sapolsky et al. 2000; McEwen and Wingfield 2003; Busch and Hayward 2009).

Studies on group size effects on glucocorticoid output yielded a heterogeneous pattern across taxa, including primates, rodents, ungulates, and birds. While the majority of studies found a positive correlation between GC secretion and group size (Foley et al. 2001; Raouf et al. 2006; Dantzer et al. 2013; Dettmer et al. 2014), there were also studies reporting opposite findings (Michelena et al. 2012; Blondel et al. 2016), or no link (Snaith et al. 2008; Ebensperger et al. 2011). In principle, both, larger and smaller groups inflict energetic costs on individuals based on resource competition and predation risks (Chapman and Chapman 2000), which in turn may cause elevated GC concentrations. Hence, individuals in groups of intermediate or "optimal" sizes may face decreased energetic constraints and exhibit the lowest GC concentrations. However, only two studies, in ring-tailed lemurs (*Lemur catta*) and yellow baboons (*Papio cynocephalus*), found optimal group size effects in GCs (Pride 2005; Markham et al. 2015). The absence of such U-shaped correlations between group size and GCs in other prior investigations might be caused by biases towards studying larger groups (Markham et al. 2015). Hence, a lack of studies taking a species' full range of group sizes into account might be one explanation for the ambiguous GC patterns found across the literature. Nevertheless, group size-related benefits and costs for social animals are complex and numerous other factors are involved in shaping the relationship between group size and health.

First, the facilitated transmission of parasites and other pathogens constitutes one of the major costs of group living (Côté and Poulin 1995; Altizer et al. 2003; Kappeler et al. 2015; Müller-Klein et al. 2018). Several meta-analyses revealed that group size and parasite transmissions are generally positively correlated, but their relationship turns out to be rather variable and complex (Altizer et al. 2003; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). This complexity is amplified by the interplay of parasites with GC secretion.

GCs can have suppressing effects on host immune function, which may lead to increased susceptibility to pathogens (Norbiato et al. 1997; Elenkov and Chrousos 1999; Turnbull and Rivier 1999). For instance, social stress in wild large vesper mice (*Calomys callosus*) caused not only elevated

GC levels, but also an impaired immune response and increased blood infections with *Trypanosoma cruzi* (Santos et al. 2008). However, the relationship between GCs and parasites seems to be reciprocal as, for example, infections with *Anguillicola novaezelandiae* in European eels (*Anguilla anguilla*) positively affected individual cortisol levels (Dangel et al. 2014). Positive associations between GCs and parasite richness were also found in chimpanzees (*Pan troglodytes*), red colobus (*Piliocolobus tephrosceles*), and black howler monkeys (*Alouatta pigra*) (Chapman et al. 2006; Muehlenbein 2006; Martinez-Mota 2015). The multidirectional relationships between social parasite transmission and GCs emphasize the strong link between sociality and health.

Second, local variation in ecological factors, either as a function of variation in habitat quality or seasonal variation in resource availability, may impact group size effects on behavioural and physiological response variables. An implicit, but crucial assumption underlying most previous tests of the *ecological constraints hypothesis* is that the habitats of different groups do not differ in structure or quality. However, small-scale habitat features, like the distribution of food patches, can affect carrying capacities of home ranges and, therefore, influence population densities and group sizes (Marsh 1981; Iwamoto and Dunbar 1983; McLean et al. 2016; Strandburg-Peshkin et al. 2017). For example, mantled guerezas (*Colobus guereza*) formed larger groups when habitats provided more food trees (Dunbar 1987). Larger prides in lions (*Panthera leo*) were more likely to occupy territories of better quality, measured via six different landscape variables (Mosser and Packer 2009), and badger (*Meles meles*) group sizes increased with the quality of food patches (Kruuk and Parish 1982). Thus, significant local habitat heterogeneity might have important implications for species' group sizes.

Here, we provide a comprehensive test of the *ecological constraints* and *optimal group size hypotheses* by examining behavioural and physiological consequences of group size variation in a wild lemur population, Verreaux's sifakas (*Propithecus verreauxi*). These endemic Malagasy primates usually live in multimale-multifemale groups, even though groups can also comprise only single males and/or females. Their groups are comparably small, ranging from 2 to 12 individuals with a mean group size of 6, yet, like other primates (Majolo et al. 2008), they exhibit up to 5-fold variation in size (Jolly et al. 1982; Kappeler and Fichtel 2012; Sussman et al. 2012; Leimberger and Lewis 2015). Over a course of 2 years, we assessed ranging, activity, and dietary patterns of seven adjacent groups. Additionally, we measured individual levels of faecal glucocorticoid metabolites (fGCMs) and examined individual parasite richness. Intestinal parasite richness seems to be generally low in Verreaux's sifakas (Muehlenbein et al. 2003; Rasambainarivo et al. 2014; Springer and Kappeler 2016). However, here we apply a metabarcoding approach to assess infestations of intestinal helminths using next-generation sequencing of 18S rRNA genes (Hadziavdic et al. 2014). Metabarcoding might be superior to previous methods, like microscopy, when assessing non-invasive parasite infestations as it allows for identification of a wide range of taxa of all life stages (i.e. eggs, larvae, and worms) and can recognize cryptic species (Aivelo and Medlar 2017).

To our knowledge, this is the first study in a mammal to simultaneously examine variation in ranging behaviour, daily activities, glucocorticoid metabolite levels, and parasitism as a function of group size while accounting for ecological stressors, namely food availability and average daily temperature differences. We expected to find one of two patterns in relation to group size: Either mean daily travel distances, home range sizes, parasite richness, and faecal GC metabolite concentrations should increase linearly with group size, according to predictions of the *ecological constraints hypothesis*, or these variables should follow a U-shaped pattern if groups of intermediate size are favoured, according to predictions of the *optimal group size hypothesis*. In case we should find heterogeneity among group habitats, we expect larger groups to inhabit areas with better quality, which should result in lower daily travel distances, foraging durations, and fGCMs for the respective groups.

Materials and methods

Study site

This study was conducted at the research station of the German Primate Center in Kirindy Forest, Western Madagascar (44° 39′ E, 20° 03′ S) from April 2016 to March 2018. Kirindy Forest is a protected dry deciduous forest and subject to pronounced seasonality, with a long, cool dry season (April to October) and a hot wet season (November to March) (Kappeler and Fichtel 2012).

Study species

We observed a total of 42 Verreaux's sifakas living in 7 adjacent groups ranging in size from 2 to 10 individuals, covering a broad range of group sizes found in this species with a maximum range of 1 to 12 individuals (Jolly et al. 1982; Sussman et al. 2012; Leimberger and Lewis 2015) (Table 1). Verreaux's sifakas are diurnal and arboreal primates with a mainly folivorous diet, but they exhibit pronounced seasonal dietary flexibility (Koch et al. 2017). They inhabit home ranges that remain stable over many years and partially overlap with those of neighbouring groups, but also include core areas of exclusive use (Benadi et al. 2008; Koch et al. 2016). All animals are habituated to human observers and individually marked with unique collars.

Table 1 Summary of study groups and data collection

Group ID	Group size (mean)	Adult ♀	Adult ♂	Juveniles (< 4 years)	Infants (< 9 months)	Focal obs. (h)	GPS days	GPS locations	No. of samples (fGCM)	No. of samples (parasites)
F1	2–4 (3)	1	1	1–2	0–1	129	732	24070	160	41
L	3–4 (4)	1	1–2	1–2	0–1	215	612	20084	307	59
G	4–6 (5)	2	1	1–2	0–1	233	729	23970	315	69
M	5–7 (5)	1–2*	2*	1–2*	0–1	168	522	17179	203	42
E	5–7 (6)	1	2–3	2–3	0–1	298	700	22998	378	82
J	5–7 (7)	2	1–2	2–3	0–1	321	531	17437	347	91
F	8–10 (10)	2	1–3	3–5	0–2	448	732	24010	619	136

*As group M was a new group, marked and added to the study population in October 2016, we could not accurately assign individuals' ages. However, based on visual signs, including male chest stains, body size, behaviour, and the presence of an infant, we inferred the age of two males and one female to be above 4 years, while one female was estimated to be 3–4 years of age

Behavioural observations

Focal animal sampling was carried out on all members of the 7 study groups, including adults and juveniles (> 9 months). Observations of 1 h per individual were conducted in an alternating order for 3 h in the morning and 3 h in the afternoon, resulting in a total of 1812 h of behavioural data. We continuously recorded all activities (social and non-social) as well as the identity of feeding plants and parts. As our study involved focal animal observations, it was not possible to record data blind.

GPS data collection

For assessing ranging patterns, one adult male per group was equipped with a GPS collar (e-obs, Grünwald, Germany) during annual captures (for details see Kappeler and Fichtel 2012). All collars were set to record GPS coordinates every 30 min between 04:00 and 20:00 h local time. As sifakas remain stationary on their sleeping tree during the night (Erkert and Kappeler 2004), we did not collect GPS locations between 20:00 and 04:00 h (Koch et al. 2016). On average, we recorded GPS data for 651 days with a mean of 21400 GPS locations per group (Table 1). For estimating home range sizes and core areas, we used monthly 95% and 50% fixed kernels using the *adehabitatHR* package (Calenge 2006) in R (R Version 3.4.4, R Core Team 2018). Daily travel distances (DTD) were calculated using the *points-to-path* plugin in Quantum GIS (QGIS Development Team 2018).

Faecal sample collection and analyses

During behavioural observations, fresh faecal samples, uncontaminated by urine, were collected within 3 min after defecation from the forest floor whenever they could be unequivocally assigned to an individual. Samples were collected weekly from all study animals except for dependent offspring.

Hormone analyses

Faecal samples for glucocorticoid metabolite (fGCM) analysis were collected in the morning between 07:00 and11:00 h (n = 2329) and placed in 15-ml polypropylene tubes (Sarstedt, Nümbrecht, Germany) containing 5 ml of 80% ethanol. fGCM concentrations were determined upon subsequent extraction by using a validated enzyme immunoassay (EIA), measuring 5ß-reduced cortisol metabolites (Fichtel et al. 2007) (for details see Online Resource 1).

Parasite analyses

A total of 520 faecal samples were collected during four periods (April–May 2016/2017 and September–October 2016/2017). We collected up to four samples (Ø 3.9) per period from each study animal. Samples were stored in 2-ml polypropylene tubes containing 1 ml RNA*later* (Thermo Fisher Scientific, Waltham, MA, USA) at ambient temperature. After 24 h, when RNA*later* had completely soaked the faeces, samples were stored in a freezer at − 20 °C and remained frozen throughout shipping to Germany, where further analysis ensued.

Extraction of DNA, amplification, and sequencing of 18S rRNA genes We conducted DNA extraction with the PowerSoil DNA isolation kit (MoBio, Carlsbad, Canada). PCR reactions to generate eukaryotic 18S rRNA gene amplicons were performed in triplicates for each sample, then pooled in equimolar amounts and cleaned. Afterwards, we conducted dual-indexed paired-end sequencing with the Illumina MiSeq platform and v3 chemistry (for details see Online Resource 1).

18S rRNA gene amplicon analyses Amplicon sequence variants (ASVs) were generated with VSEARCH version 2.9.1. We removed chimeric sequences with VSEARCH using UCHIME3 in de novo (–uchime3_denovo) and reference (–

uchime_ref) mode against the PR^2 database (version 4.11.0) (Guillou et al. 2013). The following steps were conducted with the package *ampvis2* (version 2.3.19) (Skytte et al. 2018) in R (version 3.4.4) (R Core Team 2018). We performed sample comparisons at the same surveying effort, using the lowest number of sequences by subsampling (2600 reads per sample). Additionally, we removed chloroplasts and extrinsic domains or unclassified ASVs from the data set (for details see Online Resource 1).

Habitat quality

Fixed area plots are a common sampling method in forest inventories (Scott 1998). For each group, 10 square plots (~ 25 × 25 m) within the corresponding home range were randomly selected and all trees with a larger diameter than 5 cm were identified to the species level and the diameter at breast height (DBH) was measured (for details see Online Resource 1).

For estimating habitat quality, we examined feeding tree characteristics of each home range. We compared density, species richness, and sizes of a total of 6690 feeding trees belonging to 77 different species. These species were consumed during 67 ± 4% SD of time during groups' foraging bouts. Identification of feeding tree species is based on behavioural observations from June 2016 until March 2018 and comprises 539 h of observed feeding.

Statistical analyses

GLMMs: group size effects on ranging patterns and fGCM concentrations

We applied generalized linear mixed effect models (GLMMs) (Baayen et al. 2008) from the *lme4* package (version: 1.1.21) (Bates et al. 2015) in R (version3.5.1) (R Core Team 2018), to test whether group size and group size-squared or group ID affect monthly averaged measures of DTDs, home range sizes, and individual fGCMs. We included study year (first or second), food availability, temperature differences (Δ temperature), and sex (for fGCM models only) as fixed effects to control for ecological and social influences. Food availability was based on monitoring monthly phenology of 690 trees throughout the study period. We used a semi-quantitative method (Fournier 1974) in which the availability for each plant part (i.e. leaves, fruit, flowers) was scored, ranging from 0 (complete absence) to 4 (maximum abundance) (for details, see Koch et al. 2017). Δ temperatures describe the average monthly differences between daily minimum and maximum temperatures. We also examined interactions between group size and group size-squared with food availability and Δ temperatures in all respective models, to investigate group size effects on behavioural and physiological adaptations to seasonal changes. To keep type I error rates at the nominal level of 5%, we included random slopes (Barr et al. 2013). *p* values for individual effects were based on likelihood ratio tests comparing the full with the respective null models using the *drop1* function (Barr et al. 2013). If models resulted in significant effects of group ID, we conducted Tukey post hoc tests using the *glht* function of the package *multcomp* (version 1.4-10).

GLMMs: group size effects on activity patterns

To examine effects of group size or group ID on mean monthly foraging and resting rates, we calculated binomial models with beta error distribution structures and a logit link function using the *glmmTMB* package (version 0.2.3) (Brooks et al. 2017). Response variables (foraging and resting rates), predictors (group size or group ID, food availability, Δ temperatures), control variables (study year), random effects (group and animal ID), and random slopes (group size, food availability, Δ temperatures, and study year within group and animal ID) were included the same way as described above. We conducted full-null model comparisons and estimations of *p*-values as described above. Models resulting in significant effects of group ID were further analysed by comparing predicted marginal means using the *lsmeans* function of the package *emmeans* (version 1.3.3).

In all statistical analyses, our measure of group size comprised all present individuals, including adults (age > 4 years), juveniles (age < 4 years), and dependent infants (age < 9 months) (Kappeler and Fichtel 2012). Yet, especially dependent infants may require and consume considerably less energy compared with juveniles and adults. As this could have important implications for how group size affects fGCM concentrations, activity, and ranging patterns, we re-ran all statistical analyses with a second measure of group size that excluded dependent infants (Online Resource 1, Tables S14-S18). However, we did not find differences in model outcomes when using these two different measures of group size.

Moreover, we examined correlations between group sizes and core areas. As home range sizes were highly correlated with core areas (Pearson, $r = 0.987$; $n = 22$; $p < 0.001$), we only considered home range sizes in our main analyses but added analyses on core areas to Online Resource 1 (Tables S19-S20, Fig. S3a, b).

GLMMs: correlations among fGCMs, activity, and ranging patterns

We additionally examined potential links between individual monthly fGCMs with ranging and activity patterns by applying two GLMMs as described above. We ln-transformed the response value (fGCMs) and included DTD or HR and foraging or resting rates as predictor variables. We included food

availability as control variable. Monthly Δ temperatures were correlated with DTD and HR (Pearson: DTD/ΔTemp, $r = -0.82$, $n = 22$, $p < 0.001$; HR/ΔTemp, $r - 0.55$, $n = 22$, $p < 0.001$, Fig. S4c, d), which is why we excluded them from the model. Group and animal ID were utilized as random effects; and DTD or HR, foraging or resting rates, and food availability as random slopes within group and ID, respectively.

ANOVA/Kruskal–Wallis: differences in habitat quality

For comparing feeding tree characteristics (i.e. density, species diversity, and basal areas of all feeding trees) between the habitats, we conducted one-way ANOVAS or Kruskal–Wallis tests. Significant results were further analysed with Tukey tests using the *glht* function of the package *multcomp* (version 1.4-10) or with Dunn's pairwise post hoc tests (Bonferroni correction) using the package *FSA* (version 0.8.22), respectively.

See Online Resource 1 for more details on all statistical analyses.

Results

Ranging patterns

Verreaux's sifakas inhabited home ranges with a monthly average size of 15 ± 7 ha (mean ± SD) and travelled on average 954 ± 234 m per day. The model examining effects of group size, food availability, Δ temperatures, and study year on home range sizes was significant ($\chi^2 = 43.492$, df = 9 $p < 0.001$, $R^2_{m/c} = 0.23/0.79$); however, group size was not correlated with home range size (Table S1, Fig. 1a). The second model, including group ID instead of group size as predictor variable, was also significant ($\chi^2 = 31.173$, df = 6, $p < 0.001$, $R^2_{m/c} = 0.70/0.72$) (Table S2, Fig. 2a), indicating that groups differed significantly in their home range sizes. Specifically, groups M and L had larger and group J had a smaller home range compared with the other groups (Table S5). Results of both models revealed that home range sizes were negatively correlated with food availability and Δ temperatures, which are smallest during the months of the wet season (Table S1, S2, Fig. S1a, b).

The model examining effects of group size, food availability, Δ temperatures, and study year on daily travel distances was significant ($\chi^2 = 65.410$, df = 9 $p < 0.001$, $R^2_{m/c} = 0.70/0.82$). There was an interaction effect with DTDs and Δ temperatures, i.e. during the dry season when Δ temperatures are increased, larger groups had shorter DTDs than smaller groups (test of the interaction between Δ temperatures and group size, $\chi^2 = 6.623$; df = 1; $p = 0.010$) (Table S3). The model including group ID instead of group size as predictor variable was also significant ($\chi^2 = 76.405$, df = 9, $p < 0.001$, $R^2_{m/c} = 0.77/0.81$) (Table S2, Fig. 2a) and groups differed significantly in their DTDs. Groups M and L covered longer distances than groups J and F, while group J additionally had shorter DTDs compared with all groups except F1 (Table S5). In addition, DTDs were negatively correlated with food availability and Δ temperatures, which are smallest during the months of the wet season (Tables S3, S4, Fig. S1a, c).

Daily activities

Verreaux's sifakas spent on average 47 ± 20% (mean ± SD) of their time resting and 45 ± 20% foraging. The model examining effects of group size, food availability, and Δ temperatures on monthly foraging rates was not significant ($\chi^2 = 7.379$, df = 5, $p = 0.194$) (Table S6, Fig. 1c). In contrast, the model including group ID instead of group size as predictor variable was significant ($\chi^2 = 21.997$, df = 8, $p = 0.005$) (Table S7, Fig. 2c), as group F1 and G had shorter foraging durations than several other groups (Table S10). Foraging rates were negatively correlated with Δ temperature, i.e. animals spent less time foraging during seasons with larger daily temperature changes, i.e. during the dry season (Table S7, Fig. S1a, d).

The model examining effects of group size, food availability, and Δ temperatures on monthly resting rates was not significant ($\chi^2 = 6.195$, df = 5, $p = 0.288$) (Table S8, Fig. 1d), while the model including group ID instead of group size as predictor variable was ($\chi^2 = 21.615$, df = 8, $p = 0.006$) (Table S9, Fig. 2d). Groups differed significantly in resting durations with groups F1 and G resting shorter than several other groups (Table S10). Resting rates were positively correlated with Δ temperature, i.e. animals spent more time resting during seasons with larger daily temperatures changes, i.e. during the dry season (Tables S9, Fig. S1a, e).

Faecal glucocorticoid metabolites

On average, individuals had mean monthly fGCM concentrations of 0.326 ± 0.181 μg/g (mean ± SD). Males had generally higher average fGCM concentrations (0.360 ± 0.174 μg/g) than females (0.276 ± 0.181 μg/g) (Table S11, S12). The model examining effects of group size, food availability, Δ temperatures, study year, and sex on monthly fGCM concentrations was significant ($\chi^2 = 51.406$, df = 10, $p < 0.001$, $R^2_{m/c} = 0.20/0.36$); however, group size was not correlated with FGCM concentrations (Table S11, Fig. 1e). The model including group ID instead of group size as predictor variable was also significant ($\chi^2 = 55.800$, df = 10, $p < 0.001$, $R^2_{m/c} = 0.21/0.32$), but groups did not differ in fGCM concentrations (Table S12, Fig. 2e). Sifaka's fGCM concentrations were positively correlated with food availability and Δ temperatures, i.e. which are largest during the dry season (Table S11, S12, Fig. S1, f, g).

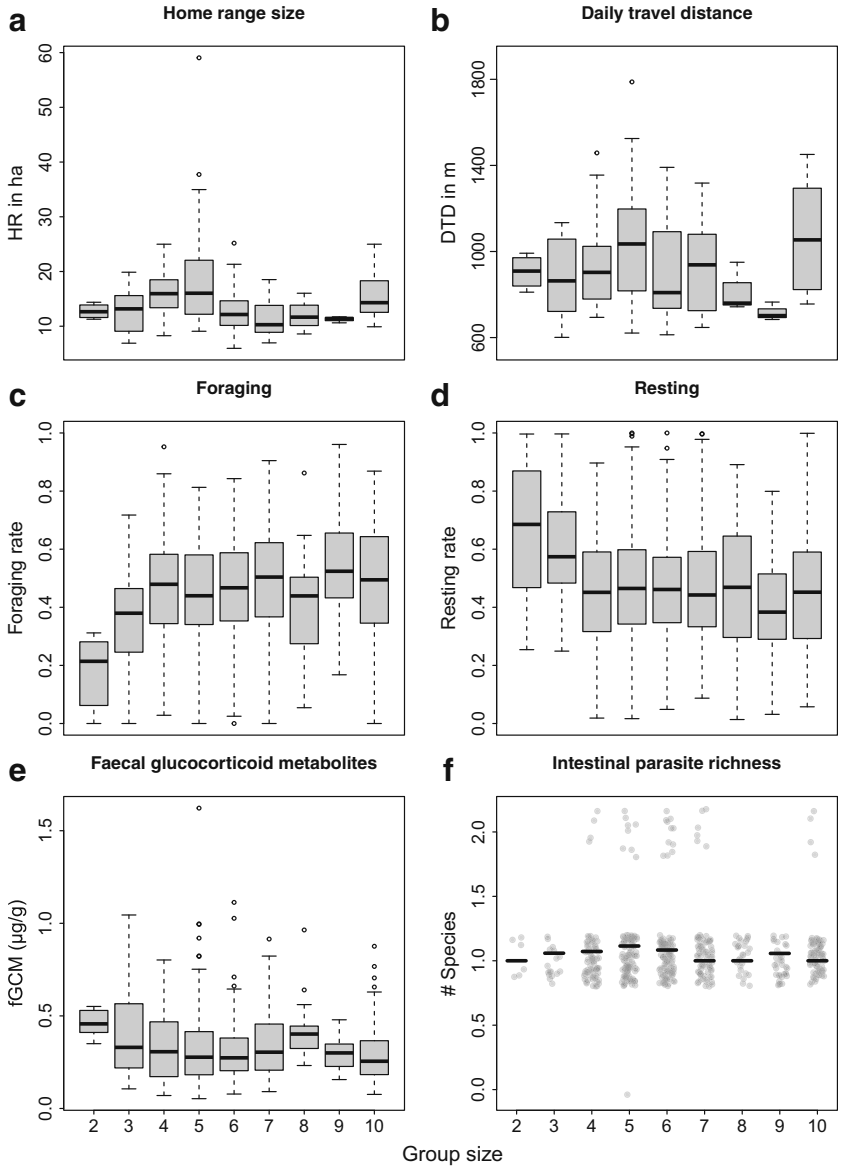

Fig. 1 Group size versus different behavioural and physiological variables. In graphs (**a**–**e**), boxplots comprise data on mean monthly rates per group (for home range size and daily travel distances) or individual (foraging, resting, fGCMs) and indicate median, upper, and lower quartiles. Whiskers indicate ± 1.5 interquartile ranges and small circles beyond whiskers indicate outliers. In graph (**f**), data points represent analysed samples and horizontal lines indicate medians

Correlations among fGCMs and activity and ranging patterns

The models on links between individual monthly fGCMs with DTDs and foraging rates or HRs and resting rates were both highly significant (DTD + foraging, $\chi^2 = 20.210$, df = 2, $p < 0.001$, $R^2_{m/c} = 0.13/0.29$; HR + resting $\chi^2 = 18.981$, df = 2, $p < 0.001$, $R^2_{m/c} = 0.14/0.31$). More precisely, DTDs and HRs were negatively correlated with fGCMs, while time spent resting was positively correlated. Foraging rates were not correlated with fGCMs (Tables S22, S23, Fig. S5).

Parasite richness

After subsampling, 33 of 520 samples were removed due to low read numbers. The remaining 487 faecal samples contained 6587 eukaryotic ASVs and 24.764.794 reads. A total of 2947 of all ASVs could be taxonomically assigned and belonged to nine phyla: *Opisthokonta* (1288), *Archaeplastida* (730), *Alveolata* (628), *Rhizaria* (194), *Amoebozoa* (116), *Stramenopiles* (36), *Hacrobia* (10), *Apusozoa* (3), and *Excavata* (2). In terms of nematodes, 3 different families known to contain parasitic species were present in the samples: *Trichostrongylidae*, *Onchocercidae*, and *Oxyuridae* (Fig. S2).

All individuals repeatedly tested PCR-positive for infestation with nematodes of the family *Trichostrongylidae* (486/487 samples). Additionally, in 33 samples from 26 individuals representing all study groups, nematodes of the family *Oxyuridae* appeared at least once ($n = 21$) and up to three times ($n = 5$) during both dry seasons. Another 32 samples of 18 individuals were positive for filarial nematodes of the family *Onchoceridae*. However, parasites of this family are

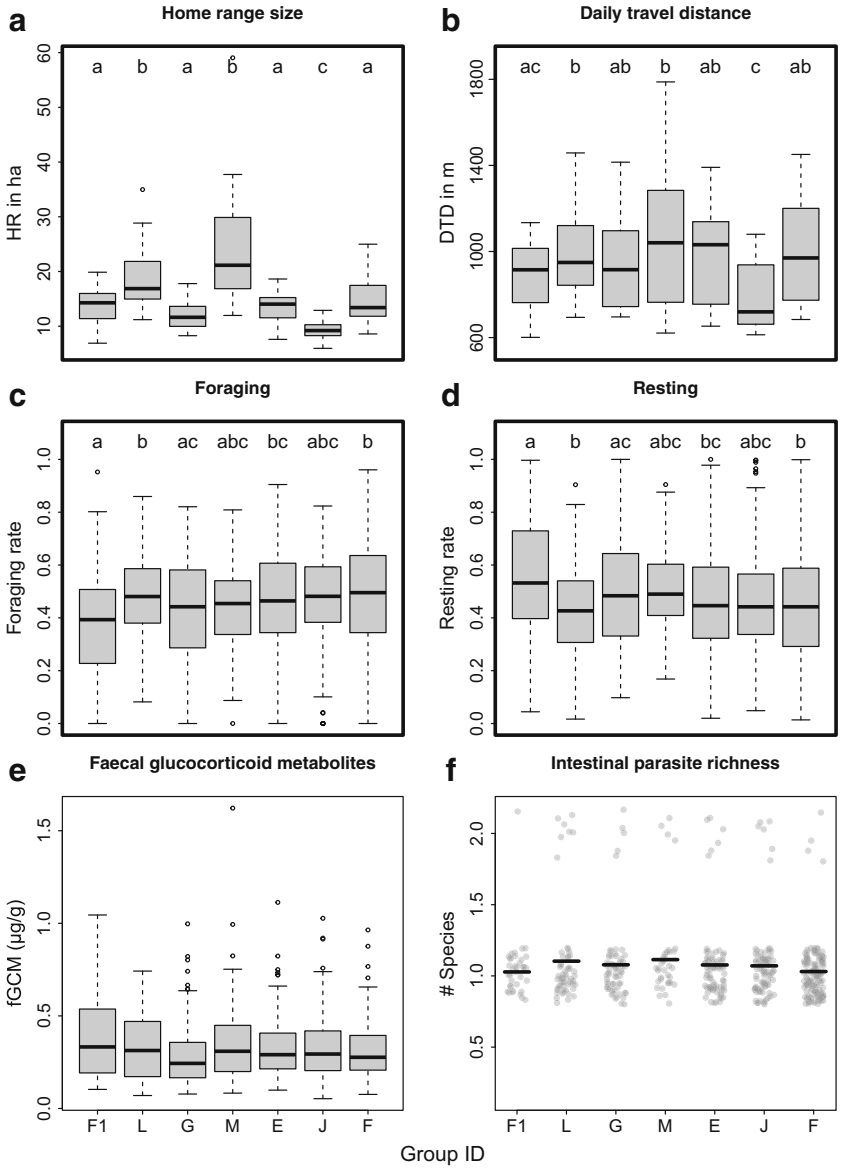

Fig. 2 Group ID versus different behavioural and physiological variables. Groups are ordered by mean group size, with the smallest group being depicted on the left. Highlighted graphs indicate significant differences among groups. Boxplots comprise data on mean monthly values per group (for home range size and daily travel distances) or individual (foraging, resting, fGCMs) and indicate median, upper, and lower quartiles. Whiskers indicate ± 1.5 interquartile ranges and small circles beyond whiskers indicate outliers. In graph (f), data points represent analysed samples and horizontal lines indicate medians. Different letters indicate significant differences in means, i.e. groups sharing at least one letter do not differ

vector-borne and usually occur in body fluids or particular tissues. Finding their DNA in faecal samples might be a result of small perforations of sifakas' intestines, leading to small amounts of blood containing the parasites entering the colon, or accidental ingestion of vectors during feeding or oral grooming. Prevalence of *Onchocercidae* was, therefore, not considered in our estimation of gastro-intestinal parasite richness. Hence, with all animals carrying *Trichostrongylidae*, and *Oxyuridae* only occurring in a few samples, intestinal parasite richness across all groups averages 1 and is not affected by group size.

Habitat quality

Groups' habitats differed in food tree density (Kruskal–Wallis, $\chi^2 = 25.723$; df = 6; $p < 0.001$) and species richness (ANOVA, $F_{6,59} = 2.34$; $p = 0.043$); however, these differences were not related to group size (Pearson: food tree density, $r = -0.287$, $n = 7$, $p = 0.533$; species richness, $r = -0.080$, $n = 7$, $p = 865$). For tree densities, post hoc Dunn's test revealed that the habitat of group M harboured significantly more trees than the habitats of groups G, J, and L. Food tree richness only differed between habitats of groups M and J, with M having a higher richness (Table S15; Fig. 3). We found no differences in food tree sizes among the different habitats (Kruskal–Wallis: *basal area*, $\chi^2 = 4.642$; df = 6; $p = 0.590$) (Fig. 3).

Discussion

In this study, we examined behavioural and physiological consequences of group size variation in wild Verreaux's sifakas.

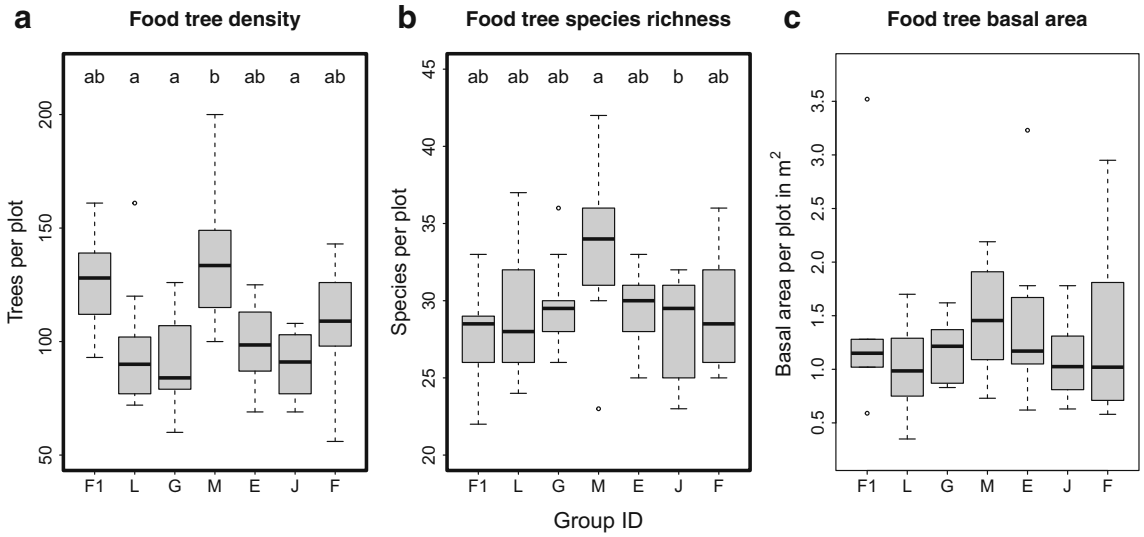

Fig. 3 Habitat characteristics of the home ranges of seven sifaka groups. Groups are ordered by mean group size, with the smallest group being depicted on the left. Boxplots show density, richness, and basal areas of the feeding trees of 10 plots per group (6 plots for group F1). Boxplots indicate median, upper, and lower quartiles. Whiskers indicate ± 1.5 interquartile ranges and small circles beyond whiskers indicate outliers. Highlighted graphs indicate significant differences among groups. Different letters indicate significant differences in means, i.e. groups sharing at least one letter do not differ

None of our measures, i.e. daily travel distances, home range sizes, foraging rates, resting rates, fGCM concentrations, and parasite richness, was correlated with group size. We detected some variation in habitat quality between groups, but this variation was unrelated to group size as well. The most important factor influencing behaviour and physiology in Verreaux's sifakas seems to be seasonality, which we operationalized via food availability and temperature differences. Altogether, our results indicate that group size on its own is insufficient to explain links between sociality and aspects of health in this lemur population.

Group size, daily activities, and habitat quality

According to the *ecological constraints hypothesis*, within-group food competition should increase in larger groups and be compensated via two key strategies: (i) longer travel distances and (ii) increased foraging durations (Chapman and Chapman 2000; Pollard and Blumstein 2008). Here, we did not find group size-related differences in ranging and activity patterns. Relying on a mainly folivorous diet, food competition may be reduced in Verreaux's sifakas compared with more frugivorous species (Janson and Goldsmith 1995; Koenig 2002). Larger groups seem not to be affected by higher costs of intra-group food competition, and smaller groups do not seem to suffer from higher costs of between-group competition. The latter notion is further supported by findings of an earlier study of the same population showing that outcomes of intergroup encounters are unrelated to group size (Koch et al. 2016). Additionally, similar fGCM concentrations across all study groups indicate no need for compensation of energetic disadvantages resulting from variation in group size. Considering that Verreaux's sifakas form relatively small groups, food competition might also not be strong enough to significantly affect individual energy budgets.

We found, however, variation in habitat quality and varying ranging patterns and daily activity among some groups. Intergroup differences in ranging behaviour have been linked to differences in local food distribution before (Caraco 1979; Altmann and Muruthi 1988; Isbell 1991; Bronikowski and Altmann 1996), and studies in baboons and three Neotropical primates revealed changes in movement patterns as a response to different habitat features (McLean et al. 2016; Strandburg-Peshkin et al. 2017). Yet, variation in habitat quality does not seem to explain different ranging and activity patterns among our study groups. For example, group M's habitat had a higher density and richness of food trees compared with group J. Hence, group M's habitat might be of better quality, which should result in reduced energetic costs due to decreased travelling and foraging efforts. Yet, group M had higher daily travel distances than group J, while there was no difference in foraging or resting rates between these two groups. It is possible that this intergroup variation could be related to locations of key food patches within the groups' habitats. While food abundance within the habitats seems sufficient to provide all groups, suboptimal distributions of preferred food trees might require some groups to travel farther then others within their home ranges. However, we did not determine exact locations of food resources and can therefore not evaluate this hypothesis.

Group size, seasonality, and fGCMs

fGCMs are often used as indicators of energetic trade-offs individuals face when living in groups (Markham and Gesquiere 2017). Life in smaller and larger groups is supposed to inflict higher energetic costs on individuals (Chapman and Chapman 2000). However, average concentrations of fGCMs did not differ with variation in group size in our study population. As none of the other measures (i.e. parasitism, ranging, and activity patterns), which might induce such energetic trade-offs, varied with group size either, these results are conclusive. Since sifaka groups did vary in ranging and activity patterns without varying in fGCM concentrations, they appear to be able to apply behavioural adaptations to environmental and/or social challenges without suffering major energetic disadvantages independent of their group size.

Notably, individual fGCM concentrations were strongly affected by seasonal variation in temperature differences and food availability. Ecological and behavioural season, however, are tightly interwined in sifakas, as the birth season falls into the middle of the cool dry season and mating season takes place around the peak of the hot wet season (Kappeler and Fichtel 2012). Thus, female reproductive state and increased energetic demands for males during the mating season (Fichtel et al. 2007) represent likely confounding factors for glucocorticoid outputs. Additionally, climatic season and unpredictability are more pronounced in Madagascar than in many other tropical regions (Dewar and Richard 2007). In Kirindy Forest, food availability is closely linked to seasonality and known to affect sifakas' diet, daily activities, and ranging patterns (Norscia et al. 2006; Koch et al. 2017). In sum, as individual variation in GC production is determined by various metabolic, social, and environmental stressors, it can be difficult to identify effects of single variables (Huber et al. 2003; Foerster and Monfort 2010).

Interestingly, ranging patterns where negatively correlated with fGCM concentrations. This finding stands in contrast to the assumption that energetically demanding behaviours, like periods of increased locomotion, are reflected in increased GC secretions (Sapolsky et al. 2000; Beehner and Bergman 2017). Both measures were correlated with seasonal changes; yet, while ranging patterns decreased with food availability and increased with temperature differences, fGCM concentrations showed opposite correlations. This suggests that Verreaux's sifakas reduce ranging activities to cope with the increased energetic requirements of thermoregulation during the middle of the dry season, when minimum and maximum temperatures differ most strongly and can fall to 3 °C (Kappeler and Fichtel 2012). These energetic requirements appear to result in increased fGCM concentrations and are potentially fortified by the low food availability during this season. The negative correlation between ranging patterns and fGCMs highlights the complexity of fGCMs patterns and emphasizes the potential of confounding factors in studies of fGCMs. In addition, we could show, similar to numerous studies in other vertebrates (Romero 2002), that sifaka's monthly fGCMs changed simultaneously with behavioural and seasonal patterns.

Group size and parasites

We detected three families of nematodes, two (*Trichostrongylidae* and *Onchocercidae*) of which have been previously reported in the same study population (Springer and Kappeler 2016) and one (*Oxyuridae*) which has been previously reported in the same species but different population (Rasambainarivo et al. 2014). Contrary to our predictions, there was no correlation between group size and intestinal parasite richness. Larger groups are expected to harbour more different parasites due to more opportunities for direct or indirect transmission via social contact or shared environments (Nunn et al. 2003). Although parasites are socially transmitted in Verreaux's sifakas (Springer and Kappeler 2016), our study animals exhibited low parasite richness, which was prevalent in almost all individuals, making it difficult to determine the mode of transmission. Hence, the costs of sociality in terms of parasite spread could not be estimated in this species.

Seasonality affected the prevalence of *Oxyuridae*, as they were only detected in samples collected during the dry season, confirming earlier results (Springer and Kappeler 2016). The dry season in Kirindy Forest represents an energetically demanding period as reflected in sifakas reduced ranging patterns and increased fGCM concentrations. It is likely that animals are more susceptible to parasites due to impaired and energetically costly immune functions during this time (Sheldon and Verhulst 1996). Given the complexity of host–parasite interactions, the effects of host group size on parasite richness might depend on various other aspects of sociality, species-specific behaviours, and environmental factors that can affect contact and, therefore, transmission rates (Patterson and Ruckstuhl 2013).

So far, only a handful of studies have used metabarcoding to non-invasively assess intestinal parasites in animals (Wimmer et al. 2004; Tanaka et al. 2014; Avramenko et al. 2015; Srivathsan et al. 2016). This novel approach can facilitate differentiation among closely related species within the same sample and, nowadays, constitutes a faster, cheaper, and more precise method in comparison with many traditional analyses (Aivelo et al. 2018). Accordingly, this approach allowed us to detect a parasite (*Oxyuridae*) that has not been found in this population before by studies using conventional microscopic methods (Springer and Kappeler 2016).

An optimal group size?

Major costs and benefits of group living are generally linked to predators, pathogens, and resource competition, which

ultimately affect individual well-being. Variation in group size reflects adaptations to local ecological conditions and represents one strategy of balancing the various advantages and disadvantages of group living. However, if, for various reasons, groups exceed their upper or lower "optimal" limits in size, the costs of sociality are expected to outweigh the benefits, and groups should, therefore, split or fusion with others (Majolo and Huang 2018).

In Verreaux's sifakas, even though groups are small with a population-wide average of 6 individuals (Jolly et al. 1982; Sussman et al. 2012; Leimberger and Lewis 2015), they varied up to 5-fold in size in our study. Yet, we did not detect substantial group size-related behavioural or physiological differences between individuals. Maybe not all assumed major costs and benefits of group living apply to this species. For example, predation risk does not seem to strongly impact Verreaux's sifakas' group sizes as another population in Berenty Reserve, where terrestrial predators are absent (Jolly 2012), exhibits a similar mean and variance in group size (Jolly et al. 1982; Norscia and Palagi 2008; Kappeler and Fichtel 2012). Additionally, due to their small groups and mainly folivorous diet, competition over food should play a less important role in shaping group size. Like other folivorous taxa, sifakas are expected to form much larger groups than they actually do. The leading hypothesis for this "folivore paradox" invokes social (i.e. male takeovers and infanticide risks) instead of ecological factors as the main constraint on group size (Treves and Chapman 1996; Steenbeek and van Schaik 2001). Thus, in Verreaux's sifakas, and perhaps other folivorous species in general, group sizes appear to remain below the upper, ecologically "optimal" limits because social rather than ecological factors define these limits. This notion may explain why we did not detect any of the group size-related costs, proposed by the *ecological constraints* and *optimal group size hypotheses*. Our findings on between-group variation in daily activities and ranging patterns suggest that differences in microhabitat features shape fine-grained behavioural adaptations. However, these behavioural differences were not reflected in groups' fGCM concentrations and parasites richness, indicating that all groups, independent of their size, can compensate potential habitat-related challenges without causing health-related costs. An optimal group size might, therefore, not exist in Verrreaux's sifakas.

Conclusions

This study contributes to the understanding of the relationship between group size, health, and ecology in vertebrates. We show that group size on its own might be insufficient to explain links between sociality and health, probably due to the complex and multifaceted nature of this relationship. We also demonstrate strong impacts of environmental factors on socio-ecological traits that might obscure patterns in the sociality-health nexus. Altogether, our results do not support predictions of the *ecological constraints hypothesis* and the *optimal group size hypothesis* as they may only hold true for species limited in group size by ecological factors—a condition that may not apply to the majority of folivorous mammals.

Acknowledgments We are grateful to the Malagasy Ministère de l'Environnement, the Departement de Biologie Ecologie et Conservation Animale de l'Université d'Antananarivo, and the Centre National de Formation, d'Etudes et de Recherche en Environnementet Foresterie de Morondava for supporting our research in Kirindy Forest. We also thank Mamy Razafindrasamba and Tiana Andrianjanahary for their support in data collection and Dr. Roger Mundry for statistical advice. We also thank two anonymous reviewers for their valuable and constructive comments. The study profited greatly from discussions with members of the DFG research unit "Sociality and Health in Primates" (FOR 2136).

Statement of authorship PMK, CF, and KR designed the study. KR and FK performed data collection. MH supervised the hormone analyses. KR conducted the lab work and analysed the data. DS helped with the analysis of the parasite data. KR drafted the manuscript and all authors contributed to writing and revising of the manuscript.

Funding information This research was financially supported by the Deutsche Forschungsgemeinschaft (DFG), grant number Ka 1082/29-2, awarded to PMK.

Data availability statement Sequences have been deposited in the NCBI GenBank under the project number PRJNA527362. All other data generated or analysed during this study are included in this published article as supplementary information files (Online Resource 2).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Statement of ethical approval, approval of research protocols, and capture procedures was approved by a committee of the Ministry for the Environment, Water and Forests of Madagascar (MINEEF) (Permit numbers: 50/16/MEEMF/SG/DGF/DAPT/SCBT.Re, 234/16/MEEF/SG/DGF/DSAP/SCB.Re, 72/17/MEEF/SG/DGF/DSAP/SCB.Re, 250/17/MEEF/SG/DGF/DSAP/SCB.Re). All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This article does not contain any studies with human participants performed by any of the authors.

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Appendix: Chapter 2

This supplementary file contains more detailed information on:

1) Supplemental Methods

A) Faecal glucocorticoid metabolite (fGCM) analyses

For fGCM analysis, faecal samples were extracted at the field site on the evening of the day the samples were collected. For steroid extraction, we manually homogenized all samples for three min and subsequently vortexed for 20 sec. Afterwards, samples were centrifuged with a manually operating centrifuge (c.f. Shutt et al. 2012; Rimbach et al. 2013) and ~1.5ml of the supernatant were decanted into 2ml polypropylene safe-lock tubes (Eppendorf®, Hamburg, Germany) for storage at ambient temperature in the dark (Rimbach et al., 2013). Faecal extracts were shipped to the Endocrinology Laboratory within one to six months following sample collection. Samples were stored at -20°C until fGCM analysis. We measured fGCM concentrations from the faecal extracts by using a group-specific enzyme immunoassay (EIA) for the measurement of 5ß-reduced cortisol metabolites (for details see Heistermann *et al.* 2004). The assay has been proven to reliably assess adrenocortical activity from faecal samples of numerous primate species of all major taxa (e.g. Heistermann *et al.* 2006), including Verreaux's sifakas (Fichtel et al., 2007). Intra- and inter-assay coefficients of variations (CVs) of high- and low-quality controls were 7.1% (high, n=17) and 8.4% (low, n=17) and 9% (high, n=75) and 16% (low, n=75), respectively.

B) Parasite richness

Extraction of DNA, Amplification, and Sequencing of 18S rRNA genes

We extracted DNA from approximately 100mg of faecal samples using the PowerSoil DNA isolation kit following the instructions of the manufacturer (MoBio, Carlsbad, Canada). However, to ensure complete homogenization of the faecal samples including parasite eggs, we used a FastPrep-24™ Classic Grinder (MP Biomedicals, Santa Ana, California, USA) instead of the suggested MO Bio Vortex adapter. Samples were homogenized for 20s at 6.5 m/s. Eukaryotic 18S rRNA gene amplicons were generated using the primers TAReuk454FWD1 and TAReukREV3 (Stoeck et al., 2010) harbouring the Illumina MiSeq sequencing adaptors. PCR reaction mixtures (total volume 50 µl) and contained 1 U Phusion high fidelity DNA polymerase (Biozym Scientific, Oldendorf, Germany), 2.5 µl DMSO (5%), 1 µl of forward and reverse 18S rRNA gene primers (10 µM), 1 µl dNTP (10 mM), 0.2 µl $MgCl_2$ (50 mM), and 50 ng of isolated DNA. Thermal cycling conditions were as follows: initial denaturation for 1 min at 98 °C, 25 cycles at 98 °C for 45 s, 60 °C for 45 s, and 72 °C for 30 s, and a final extension at 72 °C for 5 min. We included negative and positive controls (genomic DNA isolated from *Aspergillus nidulans*) in all PCRs. All PCR products were checked for appropriate size via gel electrophoresis. We performed PCR reactions in triplicates for each sample, then pooled in equimolar amounts and purified using MagSi-NGS^{PREP} Plus (Steinbrenner, Wiesenbach, Germany) as described by the supplier. Nextera DNA Library Prep kits were used for indexing PCR products according to the manufacturer's manual (Illumina), followed by dual-indexed paired-end sequencing with the Illumina MiSeq platform (2 x 300 bp) and v3 chemistry.

18S rRNA gene amplicon analyses

We demultiplexed and clipped adapters from raw sequences using CASAVA data analysis software (Illumina). Paired-end sequences were merged using PEAR v0.9.11 with default parameters (Zhang et al., 2014). Afterwards, we removed sequences with average quality scores below 20 and/or containing unresolved bases using trimmomatic 0.36. (Caporaso et al., 2010). Additionally, we employed cut-adapt 1.18 with default settings to remove reverse and forward primer sequences (Martin, 2011). Amplicon Sequence Variants (ASVs) were generated with VSEARCH version 2.9.1 (Edgar, 2010). In detail, reads were sorted by length and amplicons with a read length shorter 250 bp removed, afterwards, amplicons were dereplicated and denoised utilizing the UNOISE3 algorithm of VSEARCH. We removed chimeric sequences with VSEARCH using UCHIME3 (--uchime3_denovo) in *de novo* and reference (--uchime_ref) mode against the PR^2 database (version 4.11.0) (Guillou et al., 2013). Quality-filtered sequences were mapped to chimera-free ASVs and an ASV table was created with VSEARCH. Finally, we taxonomically classified ASVs with BLASTn against the PR^2 database.

C) Habitat quality

Forest inventories for six of the seven sifaka groups were taken in 2012 and, since the seventh group (Group M) entered the research area only by the end of 2016, another inventory was conducted in 2017 by the same field assistant. Even though sifaka home ranges are stable over years, some minor relocations still occur with time. Hence, after four years, home range location of one group (Group F1) had changed to a degree that only 6 out of 10 plots could be used for habitat comparisons. Altogether, the dataset contains 12 177 trees within 66 plots.

D) Statistical analyses

We applied 10 generalized linear mixed-effect models (GLMMs) (Baayen et al., 2008) from the package the *lme4* package (version: 1.1.21) (Bates et al., 2012) with the optimizer "bobyqa" in R (version 3.4.4) (R Core Team, 2018), to test whether group size and group size-squared or group ID affect monthly measures of daily travel distances, home range sizes, and individual fGCMs. Response values were ln-transformed to achieve roughly symmetric distributions and to avoid influential cases. In order to achieve easier interpretable models (Schielzeth, 2010) and to facilitate model convergence, we z-transformed (transformed to a mean of zero and a SD of one) all numerical variables, including predictors and random slopes. In models on group size effects, we included group size and group size-squared and their interaction with monthly temperature differences and mean monthly food availability. We included the interactions to examine group size effects on behavioural or physiological adaptations to seasonal changes. In models on the effects of group ID, no interaction was included. Monthly temperature differences, monthly food availability, study year (first or second) and sex (only for models on fGCMs) were included as fixed effects to examine ecological influences. Food availability was based on monitoring monthly phenology of 690 trees throughout the study period. We used a semi-quantitative method (Fournier, 1974) in which the availability for each plant part (i.e. leaves, fruit, flowers) was scored, ranging from 0 (complete absence) to 4 (maximum abundance) (for details, see Koch et al., 2017). Temperature differences describe the average monthly differences between daily highest and lowest temperatures. Both, food availability and temperature differences vary with season which is why we used them as proxies for seasonal effects on individual fGCMs (Figure S1a). We additionally controlled for study year (first or second). Group and animal ID (only for models on fGCMs) were utilized as random effects. To keep type I error rates at the nominal level of 5%, we included random slopes (Barr et al., 2013). For models on home range size and daily travel distance, we included random slopes of study year, food availability and temperature differences within group. For the model on fGCMs, we included the same random slopes within group and ID. Additional random slopes of group size and group size-squared were included within models testing group size effects. In models with fGCMs as response, we accounted for

the number of collected samples per individual by utilizing the argument *weights* within the *lme4* package.

Assumptions for normality distributions and homoscedasticity were checked by visually inspecting a ggplot and residuals plotted against fitted values, respectively. We did not detect obvious deviations from the assumptions for any of the models. Model stability was assessed by excluding data points one by one and comparing the derived coefficients, using a function kindly provided by Roger Mundry. This revealed no obviously influential cases. Using the function *vif* of the R-package *car* (version 3.0-2) (Fox and Weisberg, 2011) we derived Variance Inflation Factors (VIF) (Field, 2009) to a standard linear model excluding random effects. No indication of issues with collinearity among the fixed factors was found (maximum Variance Inflation Factor among all models: 2.15; Quinn and Keough, 2002). We conducted comparisons between full and null models using likelihood ratio tests (R function ANOVA with argument test set to "Chisq") (Dobson, 2002; Forstmeier and Schielzeth, 2011). Null models contained only intercepts, random effects and random slopes. We fitted the models using Maximum Likelihood rather than Restricted Maximum Likelihood (Bolker et al., 2009) to allow for likelihood ratios tests. P-values for individual effects were based on likelihood ratio tests comparing the full with respective null models using the *drop1* function (Barr et al., 2013). If models resulted in significant effects of group ID, we further analysed the effect by conducting multiple comparisons of means using Tukey contrasts with the *glht* function of the package *multcomp* (version 1.4-10). Effect sizes for the entirety of fixed and random effects of the full models were obtained with the function *r.squaredGLMM* of the package *MuMIn* (version 1.42.1) (Barton, 2018). We assessed confidence intervals with parametric bootstrapping using an adjusted function, which is based on the function *bootMer* from the *lme4* package and was provided by Roger Mundry.

To examine effects of group size or group ID on mean monthly foraging and resting rates, we conducted binomial models with beta error distribution structures and a logit link functions using the *glmmTMB* package (version 0.2.3) (Brooks et al., 2017). Response variables (foraging and resting rates), predictors (group size or group ID, food availability, temperature differences), fixed effects (study year), random effects (group and animal ID) and random slopes (food availability, temperature differences, study year, group size (in models investigating group size effects) within group and animal ID) were included the same way as described above. Due to convergence issues, we could not include group size-squared as predictor variables and, therefore, not investigate polynomial group size effects. Interactions of food availability and temperature differences with linear group sizes were included and treated as described above. We encountered no issues when checking for model stability, collinearity (maximum Variance Inflation Factor among all models: 2.20) and overdispersion. Full-null model comparisons and estimations of p-values were conducted as described above. Null models contained only intercepts, fixed effects (i.e. study year), random effects and random slopes. Models resulting in significant effects of

group ID were further analysed by comparing predicted marginal means using the *lsmeans* function of the package *emmeans* (version 1.3.3). We assessed confidence intervals with the *confint* function of the *glmmTMB* package.

2) Supplemental Results

Ranging Patterns

Home Range Size

Table S1 Influence of group size on home range size (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	2.682	0.114	2.448	2.889	2.574	2.775	[c]	[c]	[c]
Year[d]	-0.049	0.036	-0.121	0.020	-0.065	-0.018	1.693	1	0.193
Δ Temp[e]	-0.270	0.034	-0.339	-0.202	-0.304	-0.246	[c]	[c]	[c]
Food availability[f]	-0.217	0.040	-0.293	-0.130	-0.237	-0.180	[c]	[c]	[c]
Group size[g]	0.071	0.072	-0.084	0.221	-0.064	0.148	[c]	[c]	[c]
Group size^{2} [g]	-0.043	0.041	-0.131	0.046	-0.247	0.009	[c]	[c]	[c]
Δ Temp*Group size	-0.054	0.032	-0.118	0.010	-0.076	0.017	2.649	1	0.104
Δ Temp*Group size^{2}	0.026	0.020	-0.013	0.068	-0.014	0.140	1.647	1	0.199
Food avail*Group size	-0.017	0.037	-0.089	0.061	-0.027	0.036	0.245	1	0.621
Food avail*Group size^{2}	0.021	0.024	-0.029	0.069	-0.001	0.112	0.688	1	0.407

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. For intercepts, p-values would refer to estimated fGCM concentrations, when all covariates are at zero. For main effects of predictors which are involved in interaction terms, p-values refer only to the effect of that involved predictor with the interacting covariate at zero. This means the main effects of predictors involved in interactions depend on the value of the other main effects and are, therefore, not interpretable in themselves. Therefore, we consider P values of main effects to be meaningful only when the predictors are not involved in an interaction.
[d] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 5.790 and 2.072, respectively

Table S2 Influence of group size on home range size (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		2.552	0.039	2.476	2.629	2.552	2.639	[c]	[c]	[c]
Group	F	0.087	0.055	-0.019	0.197	0.086	0.087	32.95[d]	6[d]	**<0.001**[d]
	F1	0.024	0.055	-0.076	0.127	-0.063	0.024	[c]	[c]	[c]
	G	-0.090	0.055	-0.198	0.020	-0.177	-0.090	[c]	[c]	[c]
	J	-0.309	0.061	-0.437	-0.196	-0.398	-0.303	[c]	[c]	[c]
	L	0.377	0.056	0.266	0.488	0.290	0.378	[c]	[c]	[c]
	M	0.552	0.061	0.434	0.676	0.470	0.558	[c]	[c]	[c]
Δ Temp[e]		-0.251	0.024	-0.298	-0.207	-0.263	-0.240	19.656	1	**<0.001**
Food availability[f]		-0.203	0.031	-0.266	-0.147	-0.215	-0.180	15.305	1	**<0.001**
Year[g]		-0.044	0.032	-0.107	0.018	-0.061	-0.016	1.667	1	**0.197**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictor ("Group"), not the specific level indicated in the respective row
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively

Daily Travel Distances

Table S3 Influence of group size on daily travel distance (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	6.818	0.031	6.752	6.879	6.786	6.861	[c]	[c]	[c]
Year[d]	-0.048	0.020	-0.085	-0.008	-0.057	-0.027	4.285	1	**0.038**
Δ Temp[e]	-0.284	0.017	-0.317	-0.250	-0.305	-0.273	[c]	[c]	[c]
Food availability[f]	-0.159	0.017	-0.194	-0.126	-0.168	-0.145	[c]	[c]	[c]
Group size[g]	0.020	0.027	-0.039	0.078	-0.027	0.038	[c]	[c]	[c]
Group size^{2} [g]	0.006	0.018	-0.032	0.050	-0.024	0.030	[c]	[c]	[c]
Δ Temp*Group size	-0.042	0.016	-0.074	-0.011	-0.060	0.014	6.623	1	**0.010**
Δ Temp*Group size^{2}	0.021	0.011	-0.001	0.043	-0.008	0.082	3.791	1	0.052
Food avail*Group size	-0.026	0.016	-0.060	0.007	-0.035	0.003	2.422	1	0.120
Food avail*Group size^{2}	6.818	0.031	-0.007	0.036	0.003	0.041	1.769	1	0.183

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 5.790 and 2.072, respectively

Table S4 Influence of group ID on daily travel distance (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		6.853	0.022	6.807	6.896	6.853	6.865	[c]	[c]	[c]
Group	F	0.012	0.031	-0.049	0.073	0.012	0.012	22.670[d]	6[d]	**0.001**[d]
	F1	-0.080	0.031	-0.137	-0.020	-0.092	-0.079	[c]	[c]	[c]
	G	-0.041	0.031	-0.099	0.019	-0.053	-0.041	[c]	[c]	[c]
	J	-0.176	0.034	-0.244	-0.109	-0.189	-0.170	[c]	[c]	[c]
	L	0.033	0.031	-0.022	0.096	0.020	0.034	[c]	[c]	[c]
	M	0.051	0.034	-0.018	0.122	0.043	0.055	[c]	[c]	[c]
Δ Temp[e]		-0.259	0.014	-0.289	-0.231	-0.275	-0.251	30.813	1	**<0.001**
Food availability[f]		-0.143	0.013	-0.167	-0.116	-0.151	-0.132	25.954	1	**<0.001**
Year[g]		-0.051	0.020	-0.086	-0.012	-0.060	-0.031	4.694	1	**0.030**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictor ("Group"), not the specific level indicated in the respective row
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively

Table S5 Results of post-hoc multiple comparisons of means using Tukey contrasts with adjusted p-values (Bonferroni) for comparisons of home range sizes, core areas and daily travel distances among groups. Significant p-values are highlighted in bold.

Groups	Home range size		Core areas*		Daily travel distance	
	Z	p adj	Z	p adj	Z	p adj
F - E	1.570	1.000	-0.403	1.000	0.389	1.000
F1 - E	0.441	1.000	-0.854	1.000	-2.568	0.215
F1 - F	-1.129	1.000	-0.451	1.000	-2.957	0.065
G - E	-1.631	1.000	-1.213	1.000	-1.310	1.000
G - F	-3.202	**0.029**	-0.811	1.000	-1.699	1.000
G - F1	-2.073	0.802	-0.359	1.000	1.257	1.000
J - E	-5.088	**<0.001**	-2.653	0.168	-5.147	**<0.001**
J - F	-6.517	**<0.001**	-2.281	0.474	-5.499	**<0.001**
J - F1	-5.489	**<0.001**	-1.864	1.000	-2.819	0.101
J - G	-3.602	**0.007**	-1.532	1.000	-3.959	**0.002**
L - E	6.727	**<0.001**	5.185	**<0.001**	1.045	1.000
L - F	5.178	**<0.001**	5.583	**<0.001**	0.661	1.000
L - F1	6.292	**<0.001**	6.029	**<0.001**	3.579	**0.007**
L - G	8.338	**<0.001**	6.384	**<0.001**	2.338	0.407
L - J	11.186	**<0.001**	7.431	**<0.001**	6.046	**<0.001**
M - E	9.061	**<0.001**	5.538	**<0.001**	1.484	1.000
M - F	7.637	**<0.001**	5.909	**<0.001**	1.134	1.000
M - F1	8.661	**<0.001**	6.325	**<0.001**	3.794	**0.003**
M - G	10.541	**<0.001**	6.657	**<0.001**	2.663	0.163
M - J	12.936	**<0.001**	7.567	**<0.001**	6.024	**<0.001**
M - L	2.844	0.094	0.688	1.000	0.526	1.000

*Analyses and results for core areas are described at the end of this document.

Daily Activities

Foraging

Table S6 Influence of group size on foraging rates in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 659, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-0.257	0.051	-0.358	-0.157	-0.309	-0.210	[c]	[c]	[c]
Year[d]	0.098	0.044	0.012	0.184	0.064	0.124	4.775	1	**0.029**
Δ Temp[e]	-0.119	0.089	-0.293	0.054	-0.207	0.107	[c]	[c]	[c]
Food availability[f]	-0.049	0.052	-0.152	0.053	-0.108	0.049	[c]	[c]	[c]
Group size[g]	0.123	0.092	-0.057	0.304	0.077	0.187	[c]	[c]	[c]
Δ Temp*Group size	0.124	0.088	-0.048	0.296	-0.021	0.406	2.237	1	0.135
Food avail*Group size	0.018	0.055	-0.089	0.125	-0.030	0.151	0.106	1	0.745

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.525 and 0.500, respectively
[e] z-transformed, mean and SD of the original values were 16.687 and 4.278, respectively
[f] z-transformed, mean and SD of the original values were 2.803 and 0.973, respectively
[g] z-transformed, mean and SD of the original values were 6.501 and 2.169, respectively

Table S7 Influence of group ID on foraging rates in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 659, N_{ID} = 41).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		-0.224	0.088	-0.397	-0.051	-0.260	-0.138	[c]	[c]	[c]
Group	F	0.084	0.114	-0.140	0.308	0.038	0.154	17.009[d]	6[d]	**0.009[d]**
	F1	-0.498	0.164	-0.818	-0.177	-0.659	-0.356	[c]	[c]	[c]
	G	-0.291	0.135	-0.555	-0.027	-0.381	-0.203	[c]	[c]	[c]
	J	-0.092	0.124	-0.336	0.151	-0.177	0.007	[c]	[c]	[c]
	L	0.191	0.138	-0.079	0.462	-0.263	-0.047	[c]	[c]	[c]
	M	-0.167	0.152	-0.466	0.131	-0.260	-0.138	[c]	[c]	[c]
Δ Temp[e]		-0.178	0.085	-0.345	-0.011	-0.267	-0.098	3.608	1	**0.058**
Food availability[f]		-0.087	0.051	-0.188	0.013	-0.157	-0.056	2.788	1	0.095
Year[g]		0.125	0.046	0.035	0.214	0.089	0.161	6.691	1	**0.010**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictor ("Group"), not the specific level indicated in the respective row
[e] z-transformed, mean and SD of the original values were 16.687 and 4.278, respectively
[f] z-transformed, mean and SD of the original values were 2.803 and 0.973, respectively
[g] z-transformed, mean and SD of the original values were 1.525 and 0.500, respectively

Resting

Table S8 Influence of group size on resting rates in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 659, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-0.032	0.048	-0.126	0.061	-0.085	0.020	[c]	[c]	[c]
Year[d]	-0.066	0.034	-0.133	0.001	-0.086	-0.048	3.685	1	0.055
Δ Temp[e]	0.110	0.071	-0.029	0.249	-0.074	0.184	[c]	[c]	[c]
Food availability[f]	0.012	0.048	-0.082	0.107	-0.056	0.060	[c]	[c]	[c]
Group size[g]	-0.110	0.086	-0.279	0.058	-0.171	-0.070	[c]	[c]	[c]
Δ Temp*Group size	-0.070	0.074	-0.214	0.074	-0.300	0.027	0.990	1	0.320
Food avail*Group size	-0.008	0.050	-0.106	0.091	-0.100	0.020	0.024	1	0.878

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.525 and 0.500, respectively
[e] z-transformed, mean and SD of the original values were 16.687 and 4.278, respectively
[f] z-transformed, mean and SD of the original values were 2.803 and 0.973, respectively
[g] z-transformed, mean and SD of the original values were 6.501 and 2.169, respectively

Table S9 Influence of group ID on resting rates in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 659, N_{ID} = 41).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		-0.060	0.082	-0.220	0.100	-0.155	-0.032	[c]	[c]	[c]
Group	F	-0.090	0.105	-0.295	0.115	-0.157	-0.047	17.358[d]	6 [d]	**0.008** [d]
	F1	0.452	0.150	0.159	0.746	0.311	0.563	[c]	[c]	[c]
	G	0.259	0.124	0.015	0.503	0.150	0.356	[c]	[c]	[c]
	J	0.089	0.115	-0.135	0.314	0.018	0.186	[c]	[c]	[c]
	L	-0.207	0.127	-0.456	0.043	0.115	0.249	[c]	[c]	[c]
	M	0.157	0.136	-0.109	0.422	-0.155	-0.032	[c]	[c]	[c]
Δ Temp[e]		0.149	0.066	0.019	0.278	0.096	0.220	4.202	1	**0.040**
Food availability[f]		0.043	0.047	-0.050	0.135	0.013	0.098	0.820	1	0.365
Year[g]		-0.089	0.033	-0.155	-0.024	-0.104	-0.072	6.969	1	**0.008**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictor ("Group"), not the specific level indicated in the respective row
[e] z-transformed, mean and SD of the original values were 16.687 and 4.278, respectively
[f] z-transformed, mean and SD of the original values were 2.803 and 0.973, respectively
[g] z-transformed, mean and SD of the original values were 1.525 and 0.500, respectively

Table S10 Results of post-hoc comparisons of predicted marginal means with adjusted p-values (Tukey) for comparisons of foraging and resting rates among groups. Significant p-values are highlighted in bold.

Groups	Foraging rates		Resting rates	
	Estimate	p adj	Estimate	p adj
E - F	-0.084	0.991	0.090	0.978
E - F1	0.498	**0.039**	-0.453	**0.042**
E - G	0.291	0.319	-0.259	0.363
E - J	0.092	0.990	-0.089	0.987
E - L	-0.191	0.810	0.207	0.667
E - M	0.167	0.929	-0.157	0.910
F - F1	0.581	**0.004**	-0.542	**0.003**
F - G	0.375	**0.044**	-0.349	**0.038**
F - J	0.176	0.707	-0.179	0.599
F - L	-0.108	0.979	0.117	0.955
F - M	0.251	0.589	-0.247	0.449
F1 - G	-0.207	0.893	0.193	0.882
F1 - J	-0.406	0.168	0.363	0.187
F1 - L	-0.689	**0.002**	0.659	**0.001**
F1 - M	-0.330	0.559	0.296	0.559
G - J	-0.199	0.755	0.170	0.815
G - L	-0.482	**0.019**	0.466	**0.011**
G - M	-0.124	0.988	0.103	0.992
J - L	-0.283	0.371	0.296	0.227
J - M	0.075	0.999	-0.067	0.999
L - M	0.359	0.303	-0.364	0.166

Faecal Glucocorticoid Metabolites

Table S11 Influence of group size on mean monthly fGCM concentrations (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 729, N_{ID} = 42).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-1.472	0.062	-1.623	-1.317	-1.471	-1.526	[c]	[c]	[c]
Δ Temp[d]	0.354	0.037	0.243	0.459	0.354	0.332	[c]	[c]	[c]
Food availability[e]	0.126	0.036	0.021	0.231	0.126	0.100	[c]	[c]	[c]
Group size[f]	-0.024	0.060	-0.169	0.122	-0.024	-0.092	[c]	[c]	[c]
Group size^{2} [f]	0.070	0.045	-0.044	0.194	0.070	0.021	[c]	[c]	[c]
Year[g]	0.007	0.017	-0.042	0.062	0.007	-0.007	0.179	1	0.672
Sex (males)	0.308	0.073	0.135	0.472	0.307	0.272	12.352[h]	1[h]	**<0.001[h]**
Δ Temp*Group size	0.019	0.028	-0.070	0.106	0.018	-0.013	0.389	1	0.533
Δ Temp*Group size^{2}	-0.001	0.025	-0.078	0.072	0.000	-0.038	0.000	1	0.984
Food avail*Group size	0.058	0.028	-0.031	0.149	0.058	0.031	3.706	1	0.054
Food avail*Group size^{2}	-0.008	0.024	-0.085	0.072	-0.008	-0.025	0.104	1	0.747

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 16.449 and 4.264, respectively
[e] z-transformed, mean and SD of the original values were 2.804 and 0.972, respectively
[f] z-transformed, mean and SD of the original values were 6.475 and 2.155, respectively
[g] z-transformed, mean and SD of the original values were 1.551 and 0.498, respectively
[h] Values refer to the overall test of the effect of the predictor ("Sex"), not the specific level indicated in the respective row

Table S12 Influence of group ID on mean monthly fGCM concentrations (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 729, N_{ID} = 42).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		-1.442	0.091	-1.649	-1.227	-1.503	-1.376	[c]	[c]	[c]
Δ Temp[d]		0.357	0.026	0.280	0.433	0.333	0.369	26.061	1	**<0.001**
Food availability[e]		0.124	0.023	0.050	0.195	0.104	0.141	10.232	1	**0.001**
Group	F	-0.068	0.102	-0.288	0.165	-0.118	-0.022	5.602[f]	6[f]	0.469[f]
	F1	0.001	0.141	-0.322	0.322	-0.186	0.185	[c]	[c]	[c]
	G	-0.118	0.119	-0.416	0.153	-0.204	-0.037	[c]	[c]	[c]
	J	0.042	0.110	-0.216	0.300	-0.013	0.109	[c]	[c]	[c]
	L	-0.016	0.117	-0.280	0.255	-0.079	0.061	[c]	[c]	[c]
	M	0.154	0.123	-0.131	0.440	0.096	0.222	[c]	[c]	[c]
Year[g]		0.001	0.016	-0.052	0.048	-0.009	0.015	0.002	1	0.964
Sex (males)		0.332	0.066	0.177	0.479	0.309	0.354	19.655[f]	1[f]	**<0.001[f]**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 16.449 and 4.264, respectively
[e] z-transformed, mean and SD of the original values were 2.804 and 0.972, respectively
[f] Values refer to the overall test of the effect of the predictor ("Group","Sex"), not the specific level indicated in the respective row
[g] z-transformed, mean and SD of the original values were 1.551 and 0.498, respectively

Food Tree Density and Species Richness

Table S13 Results of post-hoc comparisons of groups' habitats in terms of average food tree densities and food tree species richness. Post-hoc comparisons, following a Kruskal Wallis test, of food tree densities were conducted with Dunn's pairwise post-hoc tests with Bonferroni correction. Species richness was compared with Tukey post-hoc tests, following a one-way ANOVA. Significant p-values are highlighted in bold.

Groups	Food tree density		Food tree species richness	
	Z	p adj	Estimate	p adj
E - F	-0.857	1.000	-0.500	1.000
E - F1	-2.074	0.800	-1.567	0.981
E - G	-1.332	1.000	0.500	1.000
E - J	0.839	1.000	-1.100	0.994
E - L	1.696	1.000	-0.300	1.000
E - M	2.801	0.075	4.000	0.199
F - F1	0.926	1.000	-1.067	0.998
F - G	1.783	1.000	1.000	0.996
F - J	2.876	1.000	-0.600	1.000
F - L	0.087	1.000	0.200	1.000
F - M	0.326	0.834	4.500	0.104
F1 - G	1.183	0.107	2.067	0.928
F1 - J	2.357	0.084	0.467	1.000
F1 - L	-0.513	0.387	1.267	0.994
F1 - M	-0.600	1.000	5.567	0.065
G - J	-2.913	1.000	-1.600	0.957
G - L	-2.057	1.000	-0.800	0.999
G - M	-0.449	**0.004**	3.500	0.345
J - L	-3.753	1.000	0.800	0.999
J - M	-3.840	**0.003**	5.100	**0.042**
L - M	-3.240	**0.025**	4.300	0.136

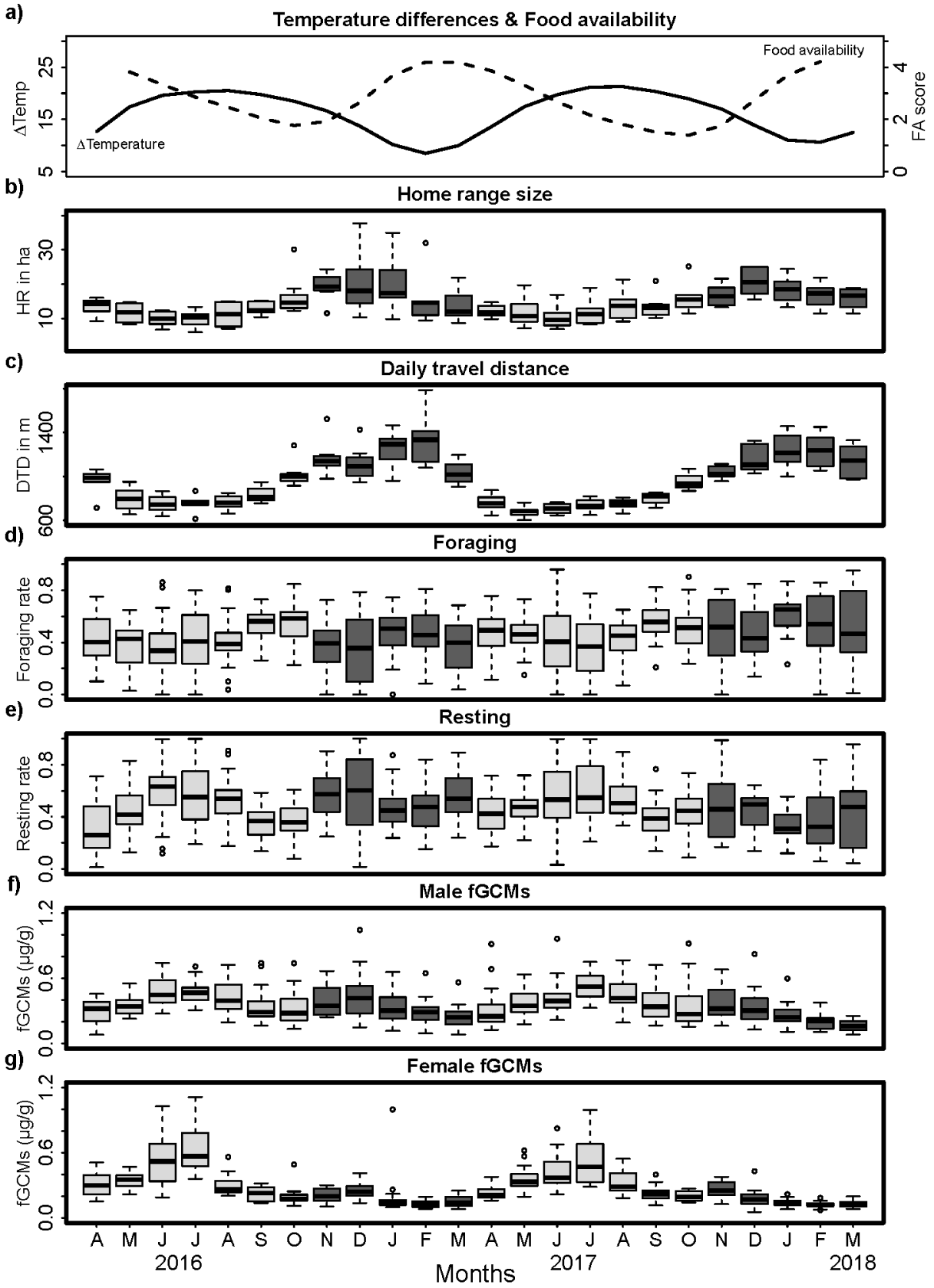


Figure S1 Effects of seasonal changes on different behavioural and physiological measures. Boxplots comprise data on mean monthly values for each group (home range size, daily travel distances) or individual (foraging, resting, fGCMs). Dark grey boxplots represent the wet season, light grey boxplots represent the dry season. Highlighted graphs indicate significant differences across the seasons. Boxplots indicate median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers.

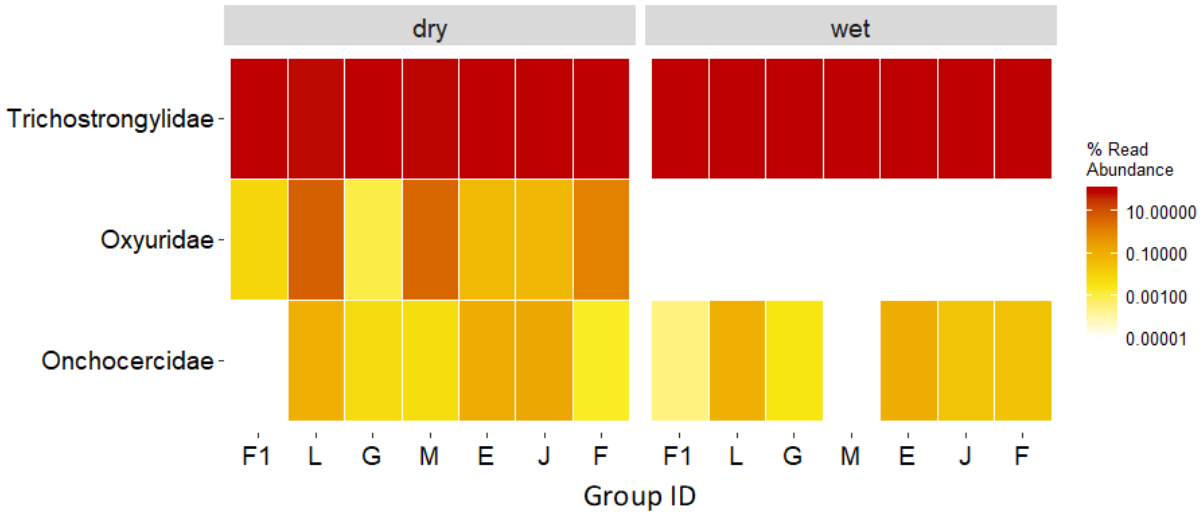


Figure S2 Abundance of three nematode families in seven neighbouring sifaka groups during dry and wet season. Data on intestinal helminth infestations were compiled with next-generation sequencing of 18S rRNA genes (N = 487 samples).

3) Further Analyses

Results of GLMMs with Group Size Measures, Excluding Dependent Infants (age < 9m):

Altogether, we did not detect major differences in group size effects in any of the five models when using two different measures of group size – one including dependent infants (see Tables S1, S3, S6, S8 & S11), and the other one excluding dependent infants (see Tables S14-S18).

Ranging Patterns

Home Range Size

The model was significant (χ^2 = 47.702, *df* = 9, *p* < 0.001, $R^2_{m/c}$ = 0.30/0.78), however, group size was not correlated to home range sizes (Table S14).

Table S14 Influence of **group size (without dependent infants)** on home range size (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^2 [b]	*df*	*P*
(Intercept)	2.572	0.108	2.372	2.799	2.488	2.641	[c]	[c]	[c]
Year[d]	-0.025	0.031	-0.086	0.035	-0.045	-0.005	0.629	1	0.428
Δ Temp[e]	-0.273	0.031	-0.335	-0.215	-0.303	-0.235	[c]	[c]	[c]
Food availability[f]	-0.209	0.038	-0.281	-0.141	-0.231	-0.175	[c]	[c]	[c]
Group size[g]	-0.094	0.088	-0.29	0.097	-0.186	-0.043	[c]	[c]	[c]
Group size^2 [g]	0.078	0.044	-0.025	0.172	-0.005	0.103	[c]	[c]	[c]
Δ Temp*Group size	-0.028	0.024	-0.076	0.019	-0.046	0.113	1.368	1	0.242
Δ Temp*Group size^2	0.019	0.019	-0.017	0.055	-0.059	0.132	0.965	1	0.326
Food avail*Group size	0.036	0.032	-0.028	0.095	0.020	0.183	1.247	1	0.264
Food avail*Group size^2	0.000	0.023	-0.046	0.048	-0.069	0.106	0.000	1	0.984

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 5.084 and 1.878, respectively

Daily Travel Distances

The model was significant (χ^2 = 65.088, *df* = 9, *p*< 0.001, $R^2_{m/c}$ = 0.67/0.83). There was an interaction effect with DTDs and Δ temperatures, i.e. during months with increased Δ temperatures, during the months of the dry season, larger groups had shorter DTDs than smaller groups (test of the interaction between Δ temperatures and group size: χ^2 = 10.229, *df* = 1, *p* = 0.001) (Table S15).

Table S15 Influence of **group size (without dependent infants)** on daily travel distance (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	6.819	0.027	6.759	6.875	6.790	6.851	[c]	[c]	[c]
Year[d]	-0.043	0.018	-0.078	-0.006	-0.056	-0.029	4.039	1	**0.044**
Δ Temp[e]	-0.278	0.017	-0.312	-0.245	-0.298	-0.261	[c]	[c]	[c]
Food availability[f]	-0.153	0.017	-0.186	-0.120	-0.162	-0.139	[c]	[c]	[c]
Group size[g]	-0.039	0.042	-0.132	0.053	-0.134	-0.001	[c]	[c]	[c]
Group size^2 [g]	0.016	0.030	-0.054	0.084	-0.105	0.068	[c]	[c]	[c]
Δ Temp*Group size	-0.043	0.013	-0.068	-0.019	-0.052	0.026	10.229	1	**0.001**
Δ Temp*Group size^2	0.018	0.011	-0.004	0.038	-0.016	0.077	2.685	1	0.101
Food avail*Group size	-0.025	0.014	-0.052	0.000	-0.029	0.012	3.276	1	0.070
Food avail*Group size^2	0.009	0.011	-0.013	0.029	-0.009	0.038	0.669	1	0.413

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 5.084 and 1.878, respectively

Daily Activities

Foraging

The model was significant (χ^2 = 13.865, *df* = 5, *p* = 0.0.016), however, group size was not correlated to foraging rates (Table S16).

Table S16 Influence of **group size (without dependent infants)** on foraging rates in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 659, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-0.270	0.042	-0.352	-0.188	-0.281	-0.251	[c]	[c]	[c]
Year[d]	0.096	0.039	0.019	0.173	0.080	0.109	5.823	1	**0.016**
Δ Temp[e]	-0.168	0.056	-0.279	-0.058	-0.207	-0.141	[c]	[c]	[c]
Food availability[f]	-0.089	0.051	-0.188	0.010	-0.134	-0.067	[c]	[c]	[c]
Group size[g]	0.103	0.047	0.010	0.195	0.079	0.125	[c]	[c]	[c]
Δ Temp*Group size	0.065	0.056	-0.046	0.175	0.013	0.103	1.304	1	0.253
Food avail*Group size	0.054	0.051	-0.045	0.154	0.011	0.077	1.139	1	0.286

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.525 and 0.500, respectively
[e] z-transformed, mean and SD of the original values were 16.687 and 4.278, respectively
[f] z-transformed, mean and SD of the original values were 2.803 and 0.973, respectively
[g] z-transformed, mean and SD of the original values were 5.781 and 1.934, respectively

Resting

The model was significant (χ^2 = 15.440, *df* = 5, *p* = 0.009), however, group size was not correlated to resting rates (Table S17).

Table S17 Influence of **group size (without dependent infants)** on resting rates in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 659, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	$\chi^{2\,b}$	*df*	*P*
(Intercept)	-0.023	0.039	-0.099	0.053	-0.042	-0.011	[c]	[c]	[c]
Year[d]	-0.067	0.034	-0.134	0.000	-0.080	-0.055	3.870	1	0.049
Δ Temp[e]	0.152	0.049	0.056	0.247	0.131	0.185	[c]	[c]	[c]
Food availability[f]	0.046	0.048	-0.047	0.139	0.029	0.082	[c]	[c]	[c]
Group size[g]	-0.093	0.044	-0.180	-0.006	-0.116	-0.071	[c]	[c]	[c]
Δ Temp*Group size	-0.025	0.050	-0.122	0.073	-0.049	0.016	0.243	1	0.622
Food avail*Group size	-0.043	0.048	-0.137	0.051	-0.064	-0.009	0.803	1	0.370

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.525 and 0.500, respectively
[e] z-transformed, mean and SD of the original values were 16.687 and 4.278, respectively
[f] z-transformed, mean and SD of the original values were 2.803 and 0.973, respectively
[g] z-transformed, mean and SD of the original values were 5.781 and 1.934, respectively

Faecal Glucocorticoid Metabolites

The model was significant (χ^2 = 56.505, *df* = 10, $p < 0.001$, $R^2_{m/c}$ = 0.26/0.50).

Table S18 Influence of **group size (without dependent infants)** on mean monthly fGCM concentrations (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 729, N_{ID} = 42).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^2 [b]	*df*	*P*
(Intercept)	-1.471	0.058	-1.610	-1.325	-1.483	-1.431	[c]	[c]	[c]
Δ Temp[d]	0.425	0.057	0.285	0.576	0.360	0.506	[c]	[c]	[c]
Food availability[e]	0.128	0.033	0.029	0.226	0.102	0.151	[c]	[c]	[c]
Group size[f]	0.083	0.066	-0.131	0.284	-0.027	0.104	[c]	[c]	[c]
Group size^2 [f]	0.127	0.093	-0.091	0.361	-0.004	0.177	[c]	[c]	[c]
Year[g]	-0.001	0.018	-0.057	0.055	-0.011	0.009	0.005	1	0.941
Sex (males)	0.328	0.067	0.173	0.476	0.305	0.348	17.644[h]	1[h]	**<0.001[h]**
Δ Temp*Group size	0.096	0.041	-0.019	0.221	0.014	0.245	2.505	1	0.113
Δ Temp*Group size^2	-0.031	0.028	-0.121	0.058	-0.047	0.014	1.191	1	0.275
Food avail*Group size	0.011	0.025	-0.076	0.091	-0.003	0.209	0.174	1	0.677
Food avail*Group size^2	-0.003	0.022	-0.071	0.067	-0.023	0.127	0.052	1	0.819

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 16.449 and 4.264, respectively
[e] z-transformed, mean and SD of the original values were 2.804 and 0.972, respectively
[f] z-transformed, mean and SD of the original values were 5.739 and 1.919, respectively
[g] z-transformed, mean and SD of the original values were 1.551 and 0.498, respectively
[h] Values refer to the overall test of the effect of the predictor ("Sex"), not the specific level indicated in the respective row

Results of Correlations between Core Areas and Group Sizes or Group IDs

Mean monthly core area sizes (50% Kernels) and home range sizes (95% Kernels) of all groups were highly correlated in Verreaux's sifakas (Pearson: r = 0.987, n = 22, $p < 0.001$), which is why we only considered home range sizes in our main analyses. Here, we report the analyses and results of correlation between group size or group ID with core area sizes.

We applied GLMMs in the same way as described above for the models on home range sizes. We ln-transformed the response (core areas) and used group ID as random effect. Z-transformed group size and group size-squared or group ID, food availability, temperature differences and study year comprised predictor variables and random slopes within group ID.

Group Size (incl. Dependent Infants) vs. Core Areas

Core areas in Verreaux's sifakas' home ranges had monthly average sizes of 4.01 ± 1.96 ha. The model examining effects of group size, food availability, temperature differences and study year on core area sizes was significant ($\chi^2 = 50.550$, $df = 9$, $p < 0.001$, $R^2_{m/c} = 0.44/0.69$), however, group size was not correlated to core area sizes (Table S19, Fig. S3a).

Table S19 Influence of group size on core area sizes (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations} = 143$, $N_{ID} = 41$).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	$\chi^{2\,b}$	*df*	*P*
(Intercept)	1.322	0.098	1.124	1.517	1.230	1.400	[c]	[c]	[c]
Year[d]	-0.015	0.028	-0.073	0.044	-0.029	0.008	0.283	1	0.595
Δ Temp[e]	-0.417	0.044	-0.508	-0.327	-0.448	-0.399	[c]	[c]	[c]
Food availability[f]	-0.272	0.043	-0.356	-0.178	-0.316	-0.243	[c]	[c]	[c]
Group size[g]	0.004	0.074	-0.158	0.162	-0.097	0.060	[c]	[c]	[c]
Group size$^{2\,g}$	-0.037	0.046	-0.138	0.064	-0.206	-0.006	[c]	[c]	[c]
Δ Temp*Group size	-0.054	0.039	-0.132	0.022	-0.081	0.013	1.780	1	0.182
Δ Temp*Group size^2	-0.010	0.027	-0.061	0.042	-0.038	0.087	0.146	1	0.702
Food avail*Group size	-0.016	0.040	-0.101	0.068	-0.040	0.049	0.159	1	0.690
Food avail*Group size^2	-0.023	0.027	-0.077	0.027	-0.034	0.071	0.682	1	0.409

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 5.790 and 2.072, respectively

Group Size (excl. Dependent Infants) vs. Core Areas

The model examining effects of group size (without dependent infants), food availability, temperature differences and study year on core area sizes was significant (χ^2 = 54.238, *df* = 9, $p < 0.001$, $R^2_{m/c}$ = 0.44/0.71), however, group size was not correlated to core area sizes (Table S20).

Table S20 Influence of **group size (without dependent infants)** on core area sizes (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	$\chi^{2\,b}$	*df*	*P*
(Intercept)	1.230	0.100	1.044	1.429	1.167	1.292	[c]	[c]	[c]
Year[d]	0.000	0.028	-0.059	0.056	-0.016	0.025	0.000	1	0.999
Δ Temp[e]	-0.411	0.041	-0.490	-0.334	-0.440	-0.369	[c]	[c]	[c]
Food availability[f]	-0.262	0.040	-0.341	-0.179	-0.311	-0.235	[c]	[c]	[c]
Group size[g]	-0.074	0.087	-0.261	0.108	-0.181	-0.036	[c]	[c]	[c]
Group size$^{2\,g}$	0.065	0.038	-0.026	0.153	0.033	0.076	[c]	[c]	[c]
Δ Temp*Group size	-0.023	0.032	-0.089	0.038	-0.036	0.127	0.518	1	0.472
Δ Temp*Group size^2	-0.015	0.026	-0.066	0.039	-0.112	0.107	0.318	1	0.573
Food avail*Group size	0.032	0.033	-0.033	0.094	0.015	0.175	0.927	1	0.336
Food avail*Group size^2	-0.030	0.026	-0.079	0.024	-0.105	0.077	1.299	1	0.254

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 5.084 and 1.878, respectively

Group ID vs. Core Areas (50% Kernels)

The model examining effects of group ID, food availability, temperature differences and study year on core area sizes was significant (χ^2 = 74.139, *df* = 9, $p < 0.001$, $R^2_{m/c}$ = 0.70/0.71), and groups differed significantly in their core area sizes (Table S21, Fig. S3b). More precisely, Groups M and L had larger core areas compared to all other groups (Table S5).

Table S21 Influence of group size on core area sizes (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 143, N_{ID} = 41).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		1.225	0.053	1.123	1.328	1.195	1.225	[c]	[c]	[c]
Group	F	-0.030	0.075	-0.191	0.117	-0.030	-0.030	27.033[d]	6[d]	<0.001[d]
	F1	-0.064	0.075	-0.219	0.086	-0.064	-0.034	[c]	[c]	[c]
	G	-0.091	0.075	-0.245	0.044	-0.091	-0.061	[c]	[c]	[c]
	J	-0.216	0.081	-0.373	-0.069	-0.224	-0.182	[c]	[c]	[c]
	L	0.395	0.076	0.245	0.541	0.395	0.424	[c]	[c]	[c]
	M	0.452	0.082	0.285	0.606	0.442	0.482	[c]	[c]	[c]
Δ Temp[e]		-0.424	0.031	-0.479	-0.364	-0.439	-0.405	29.494	1	<0.001
Food availability[f]		-0.288	0.032	-0.349	-0.226	-0.318	-0.270	21.705	1	<0.001
Year[g]		-0.015	0.024	-0.061	0.033	-0.029	0.005	0.371	1	0.542

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictor ("Group"), not the specific level indicated in the respective row
[e] z-transformed, mean and SD of the original values were 16.398 and 4.269, respectively
[f] z-transformed, mean and SD of the original values were 2.811 and 0.967, respectively
[g] z-transformed, mean and SD of the original values were 1.503 and 0.502, respectively

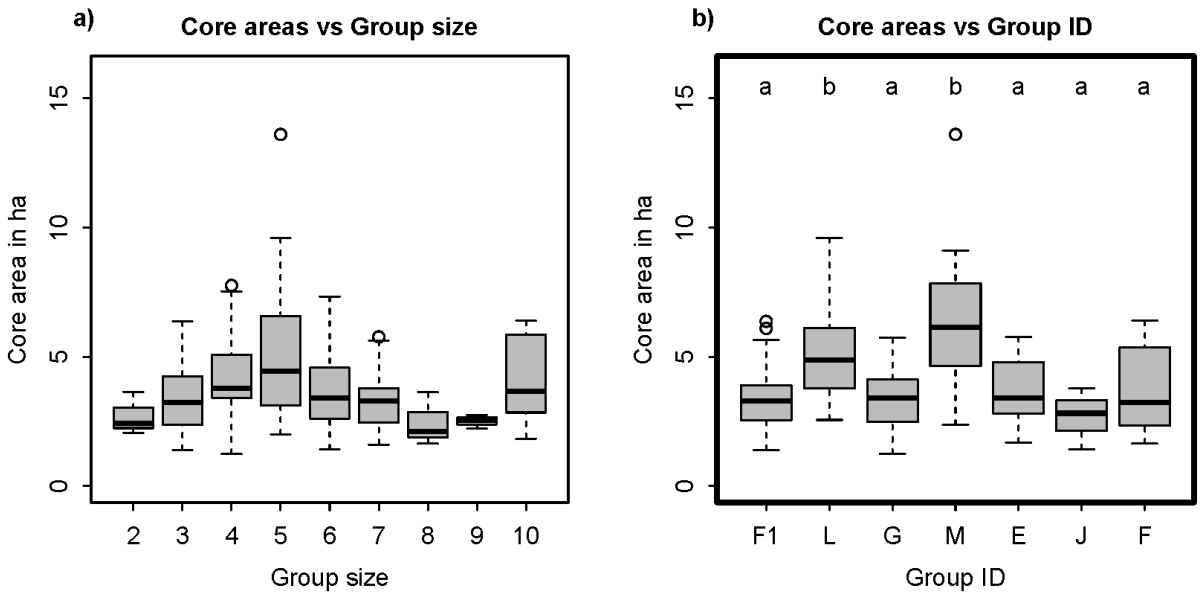


Figure S3 Group size and group ID versus core area sizes. Boxplots comprise data on mean monthly rates per group and indicate median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers. Different letters indicate significant differences in means, i.e. groups sharing at least one letter do not differ. Highlighted graphs indicate significant differences among groups or group sizes.

Results of Correlations among FGCMs, Activity and Ranging Patterns

Here, we examined potential links among the behavioural and physiological measures we collected to study effects of group size variation on Verreaux's sifakas. Of these measures, fGCMs probably represent the best indicators for individual condition. FGCMs can be directly or indirectly affected by both, behavioural (foraging, resting or ranging) and ecological (temperature differences, food availability) variables (Dunn et al., 2013; Emery Thompson, 2017). We, therefore, investigated potential coherences among these variables to enhance the general understanding of how, if at all, these factors are related to each other in Verreaux's sifakas.

We applied generalized linear mixed-effect models (GLMMs) in the same manner as described above (see methods), to test whether individual mean monthly fGCMs (response variable) are correlated to monthly daily travel distances (DTD), monthly home range sizes (HR), monthly resting and foraging rates. We ran two models, the first one including DTD and foraging rates, the second one including HR and resting rates as predictors. We had to separate monthly measures of DTD and HR, and foraging and resting rates, as these variables are highly correlated with each other (Pearson: HR/DTD: r = 0.86, n = 22, $p < 0.001$; foraging/resting: r -0.91, $p < 0.001$, Figure S4a & b), which would cause issues with collinearity

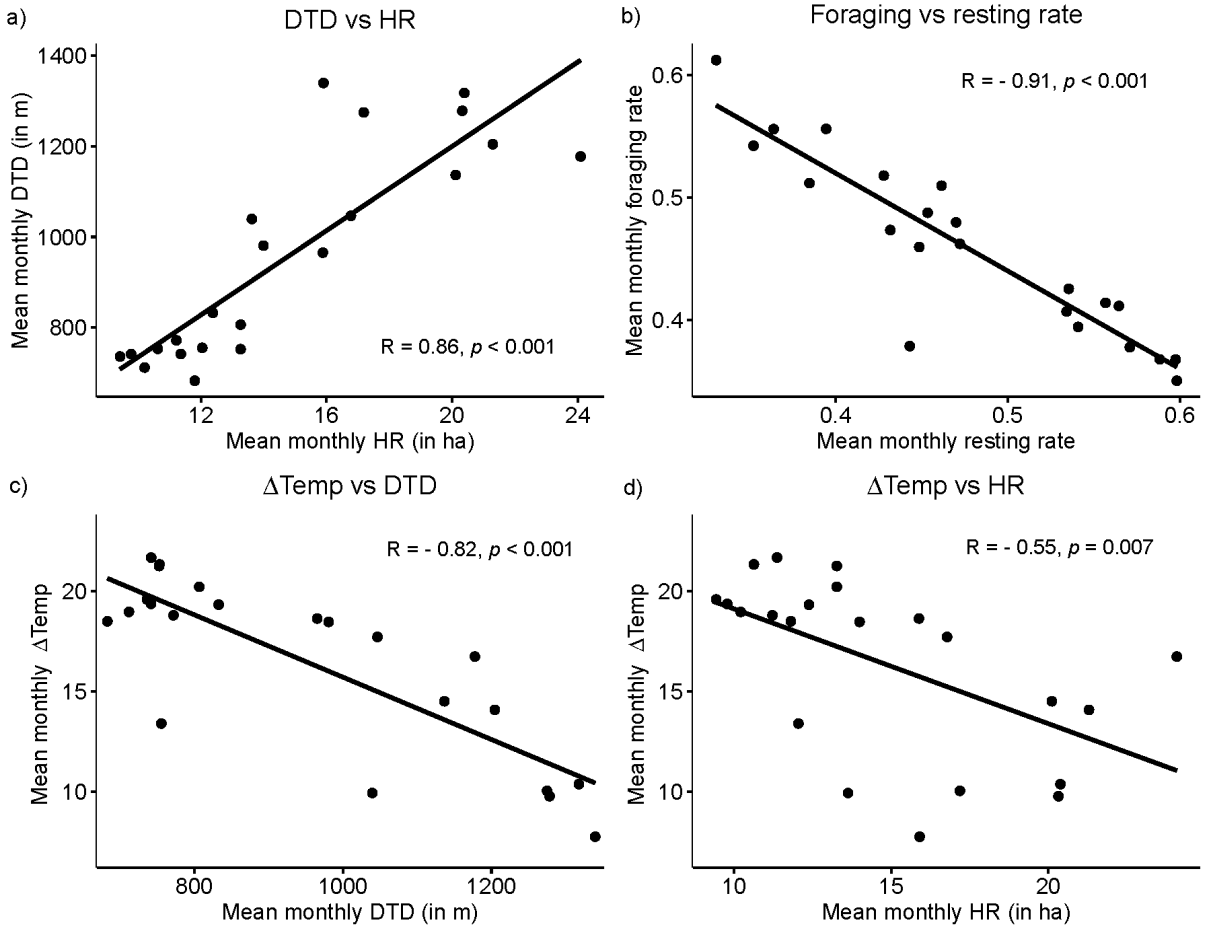


Figure S4 Pearson correlations among temperature differences, ranging and activity patterns. Data points represent monthly means of the whole study population. Solid lines represent regression lines of Pearson correlations.

(Quinn and Keough, 2002). We included food availability as control variable. Temperature differences were correlated to DTD and HR (Pearson: DTD/ΔTemp: r = -0.82,n = 22, $p < 0.001$; HR/ΔTemp: r -0.55, n = 22, $p < 0.001$, Figure S4c & d), which is why we excluded it from the model. We conducted full-reduced model comparisons, with reduced models containing intercepts, control variables (i.e. food availability), random effects and random slopes. We included group and animal ID as random effects; and DTD or HR, foraging or resting rates, and food availability as random slopes within group and ID, respectively.

Table S22 Correlations of fGCMs (ln-transformed) with mean monthly daily travel distances and foraging rates of seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 630, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-1.235	0.042	-1.325	-1.141	-1.260	-1.206	[c]	[c]	[c]
DTD[d]	-0.234	0.038	-0.325	-0.15	-0.263	-0.206	12.694	1	**<0.001**
Foraging rate[e]	-0.047	0.016	-0.102	0.009	-0.057	-0.037	6.563	1	0.010
Food availability[f]	-0.061	0.029	-0.132	0.012	-0.078	-0.033	3.467	1	0.063

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 918 and 238, respectively
[e] z-transformed, mean and SD of the original values were 0.454 and 0.192, respectively
[f] z-transformed, mean and SD of the original values were 2.800 and 0.962, respectively

Table S23 Correlations of fGCMs (ln-transformed) with mean monthly home range sizes and resting rates of seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$= 630, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-1.229	0.066	-1.375	-1.09	-1.279	-1.189	[c]	[c]	[c]
HR[d]	-0.264	0.048	-0.389	-0.142	-0.310	-0.239	11.626	1	**0.001**
Resting rate[e]	0.077	0.021	0.012	0.143	0.060	0.093	7.562	1	**0.006**
Food availability[f]	-0.101	0.031	-0.179	-0.030	-0.114	-0.068	6.548	1	**0.011**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 14.163 and 6.310, respectively
[e] z-transformed, mean and SD of the original values were 0.482 and 0.195, respectively
[f] z-transformed, mean and SD of the original values were 2.800 and 0.962, respectively

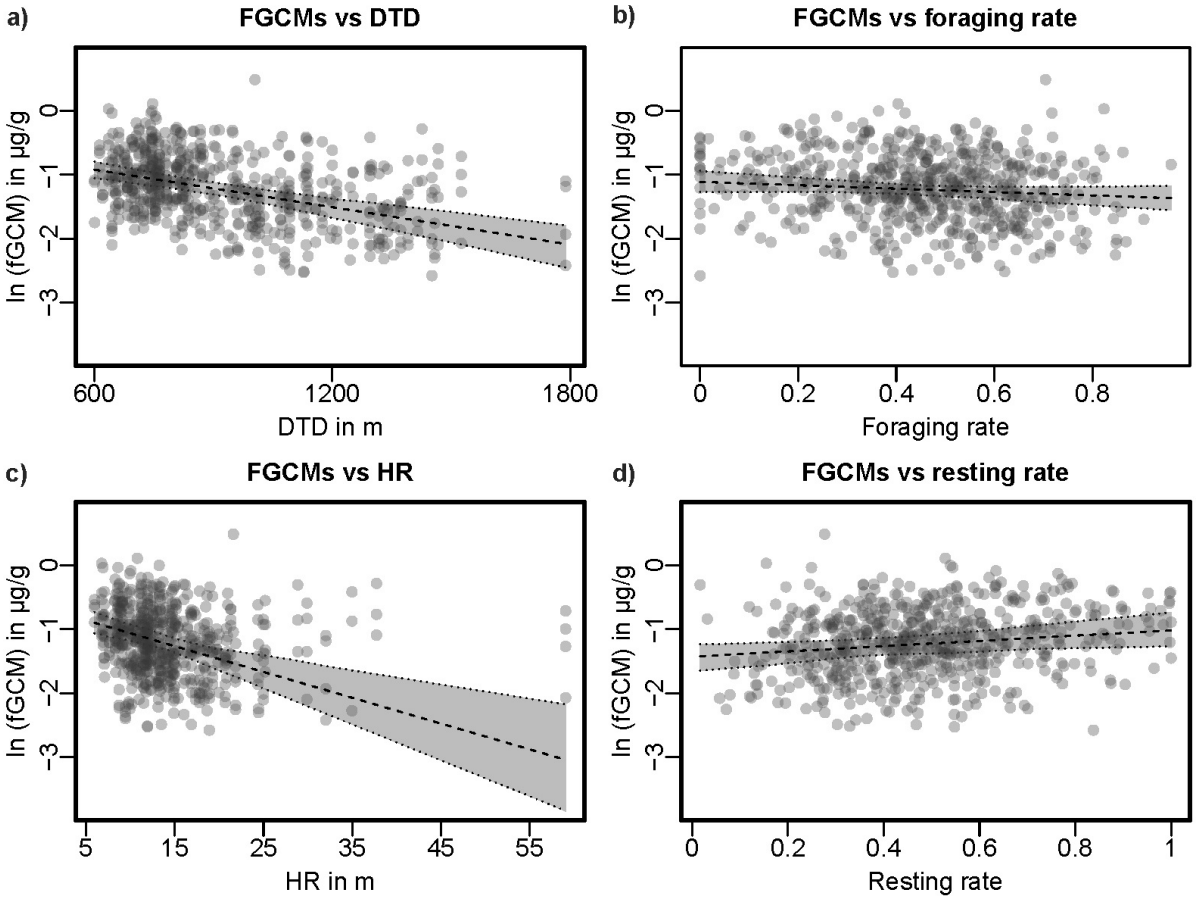


Figure S5 Correlations of individual monthly fGCMs with ranging and activity patterns. Data points represent monthly means of the corresponding variable. Dashed lines represent regression lines of the models and grey areas mark confidence intervals. Highlighted graphs indicate significant correlations.

Chapter 3

Study II

Dynamics and Determinants of Glucocorticoid Metabolite Concentrations in Wild Verreaux's Sifakas

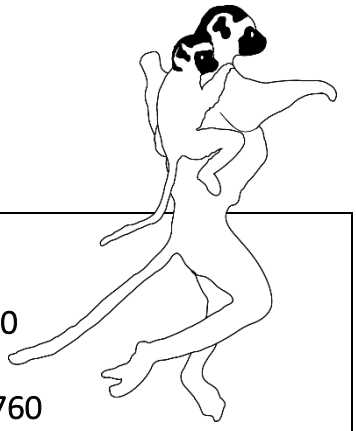
with Claudia Fichtel[1,3], Michael Heistermann[4], and Peter M. Kappeler[1,2,3]

[1] Behavioral Ecology & Sociobiology Unit, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[2] Dept. Sociobiology /Anthropology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology, University Göttingen, Göttingen, Germany

[3] Leibniz Science Campus "Primate Cognition", Göttingen, Germany

[4] Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

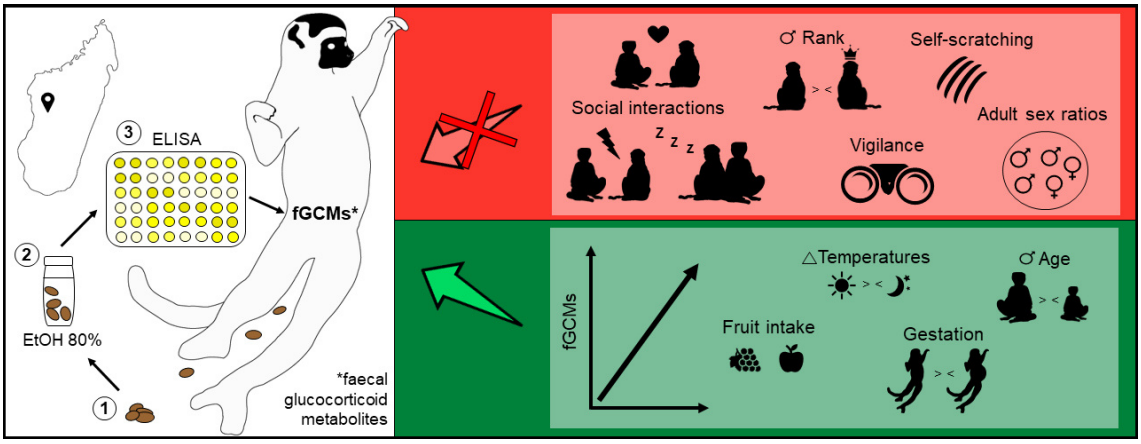


This chapter is published in

Hormones & Behavior (2020) 124: 104760

https://doi.org/10.1016/j.yhbeh.2020.104760

Graphical Abstract



Abstract

Glucocorticoids have wide-ranging effects on animals' behaviour, but many of these effects remain poorly understood because numerous confounding factors have often been neglected in previous studies. Here, we present data from a 2-year study of 7 groups of wild Verreaux's sifakas (Propithecus verreauxi), in which we examined concentrations of faecal glucocorticoid metabolites (fGCMs, n = 2350 samples) simultaneously in relation to ambient temperatures, food intake, rank, reproduction, adult sex ratios, social interactions, vigilance and self-scratching. Multi-variate analyses revealed that fGCM concentrations were positively correlated with increases in daily temperature fluctuations and tended to decrease with increasing fruit intake. fGCM concentrations increased when males were sexually mature and began to disperse, and dominant males had higher fGCM concentrations than subordinate males. In contrast to males, older females showed a non-significant trend to have lower fGCM levels, potentially reflecting differences in male and female life-history strategies. Reproducing females had the highest fGCM concentrations during late gestation and had higher fGCM levels than non-reproducing females, except during early lactation. Variation in fGCM concentrations was not associated with variation in social interactions, adult sex ratios, vigilance and self-scratching. Altogether, we show that measures of glucocorticoid output constitute appropriate tools for studying energetic burdens of ecological and reproductive challenges. However, they seem to be insufficient indicators for immediate endocrinological responses to social and nonsocial behaviours that are not directly linked to energy metabolism.

Chapter 4

Study III

Exploring causes for gut microbiome variation among groups of wild Verreaux's sifakas

with Dominik Schneider[1], Claudia Fichtel[2,4], Rolf Daniel[1],

and Peter M. Kappeler[2,3,4]

[1] Genomic and Applied Microbiology and Göttingen Genomics Laboratory, Institute of Microbiology and Genetics, University Göttingen, Göttingen, Germany

[2] Behavioral Ecology & Sociobiology Unit, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

[3] Dept. Sociobiology /Anthropology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology, University Göttingen, Göttingen, Germany

[4] Leibniz Science Campus "Primate Cognition", Göttingen, Germany

In preparation for submission

Abstract

The gut microbiota plays a fundamental role for animal health and the identification of ecological and evolutionary processes shaping host-associated microbial communities constitutes a key topic in molecular ecology. An increasing number of studies have reported associations between group living and gut microbial convergence, however, the relative contributions of environmental, intrinsic and social factors to these links remain debated. Here, we examine the drivers of gut microbial convergence among seven neighbouring groups of wild Verreaux's sifakas (*Propithecus verreauxi*) - a group-living primate from Madagascar. Over four field seasons, we collected 519 faecal samples of 41 animals and determined gut microbial composition and diversity via 16S rRNA gene sequencing. We correlated microbial data with observations of social interactions, maternal relatedness, diet, habitat structure and overlap, while controlling for seasonality. Groups differed in both, composition and diversity of their gut microbiomes. In contrast to most primate studies, we found kinship to play an important role for within-group microbial homogeneity, while we did not find an effect of dyadic social contact. None of the environmental predictors explained variation in microbial communities between groups. Altogether, we find that environmental factors define the general set-up of species- or population-specific gut microbiota, while kinship has important implications for individual microbial patterns. The degree to which social interactions shape individual gut microbiota seems to differ with species' social systems, which determine opportunities for microbial dispersals. More comprehensive research on taxa with varying social systems will help to understand the co-evolutionary dynamics of host sociality and microbial transmission strategies.

Introduction

As animal life emerged and evolved in a microbial world, it is not surprising that their bodies are home to diverse assemblages of microbes. These microbes have important functions in the context of maintaining and shaping their host's condition and health. Gut bacteria, for example, are involved in digestion and energy harvest (Gill et al., 2006; Turnbaugh et al., 2006b), they interact with the immune system (Chow et al., 2010; Kinross et al., 2011), and cases of dysbiosis are associated with lower serum immunoglobulin levels, decreased lymphocytes (Round and Mazmanian, 2009) and several diseases, like diabetes (Boerner and Sarvetnick, 2011) and Crohn's disease (Knights et al., 2013). However, the relationship between gut microbiota and their hosts is bi-directional and dynamic, as the microbial compositions are shaped by various social, genetic and environmental factors (Clayton et al., 2018; Gogarten et al., 2018; Grieneisen et al., 2019; Heitlinger et al., 2017; Ren et al., 2017). In the last decade, much progress has been made towards identifying the forces that shape host-microbiota relationships in humans and laboratory animals, but only more recently attention was given to studies of wild animals. Yet, identifying the factors that drive differences in gut microbiota composition in wild populations is critical for understanding how microbes impact animals' health, ecology and evolution under natural conditions (Björk et al., 2019), not the least because gut microbiomes play a key role in mediating links between sociality and health (Archie and Theis, 2011; Clayton et al., 2018; Kappeler et al., 2015).

Social drivers of gut microbiome communities

An increasing number of studies across different taxa, ranging from insects over birds to mammals, has reported associations between microbiome composition and social co-residency (Ezenwa et al., 2012; Levin et al., 2016; Martinson et al., 2011; Raulo et al., 2017; Song et al., 2013; Springer et al., 2017; Trosvik et al., 2018). Increased physical contact between group members facilitates the transmission of microorganisms and is a prevalent mechanism for shaping distinct group microbiomes (Kulkarni and Heeb, 2007; Moeller et al., 2016; Raulo et al., 2017; Tung et al., 2015). It may also facilitate transmission of pathogen resistance-enhancing bacteria (Ezenwa et al., 2016; Hughes et al., 2002; Koch and Schmid-Hempel, 2011; Kuthyar et al., 2019) and can increase microbial diversity, which is suggested to correlate with resilient immunity (Hooper et al., 2012; Lozupone et al., 2012). Within groups, affiliative interactions between individuals can result in convergence in microbial communities, as shown in baboons (*Papio cynocephalus*), howler monkeys (*Alouatta pigra*) and humans (Amato et al., 2017a; Lax et al., 2014; Tung et al., 2015). However, group membership or social contact are not always linked to variation in gut microbiome compositions, as reported in fruit bats (*Rousettus aegyptiacus*) (Kolodny et al., 2019) or sooty mangabeys (*Cercocebus atys*) (Gogarten et al., 2018).

Group size represents another aspect of sociality that can alter microbial compositions and diversities (Turnbull et al., 2011) because variation in group size can affect frequencies of social

interactions and physical contacts (Keiser et al., 2018; Nunn et al., 2015). Accordingly, population density in plateau pikas (*Ochotona curzoniae*) and group size in yellow baboons were found to be positively correlated with microbiome diversity (Grieneisen et al., 2017; Li et al., 2016), whereas group size was negatively correlated in African social spiders (*Stegodyphus dumicola*) (Keiser et al., 2018) or not correlated in red-bellied lemurs (*Eulemur rubriventer*) (Raulo et al., 2017). Hence, the effects of social contact and group size on microbial diversity remain ambiguous across taxa. Moreover, the relative contributions of sociality in shaping gut microbial communities against the background of variation in genetic and environmental factors remain little understood, especially in wild populations.

Kinship as driver of gut microbiome communities

Kinship can influence similarity of gut microbiomes among individuals (Lombardo, 2008; Yuan et al., 2015; Zoetendal et al., 2001). There are three known mechanisms underlying this effect: 1) heritability of microbiomes, i.e. inheritance of certain genetic loci, under the premise that host genomes dictate to some degree abundances of microbes (Goodrich et al., 2014; Kovacs et al., 2011; Opstal and Bordenstein, 2015); 2) direct maternal transmission to offspring *in utero* (e.g. Collado et al., 2016; but see Perez-Muñoz et al., 2017) or during delivery (Bokulich et al., 2016; Gregory et al., 2015); or 3) transmission via physical contacts in the contexts of parental care and social behaviours (Funkhouser and Bordenstein, 2013; Lombardo, 2008). Microbial patterns obtained via one of the afore-mentioned transmission modes can persist into adulthood (Nelson et al., 2013; Palmer et al., 2007; Ren et al., 2017). Yet, there is little knowledge on the contribution of kinship to microbial composition and diversity in wild populations. So far, studies in red squirrels (*Tamiasciurus hudsonicus*), cheetahs (*Acinonyx jubatus*) and gopher tortoises (*Gopherus polyphemus*) (Yuan et al., 2015; Ren et al., 2017; Wasimuddin et al., 2017) found strong indications for kinship effects on gut microbiomes, whereas studies in baboons, chimpanzees and howler monkeys found either no or only weak links (Amato et al., 2017a; Degnan et al., 2012b; Grieneisen et al., 2017). This variation may be due to the fact that groups contain variable numbers of related individuals, and the frequency and nature of social interactions varies among species.

Environmental drivers of gut microbiome communities

Environmental factors, like host diet and habitat heterogeneity, are well known to affect animals' gut microbiomes as well (Greene et al., 2019b; Kohl et al., 2017; Perofsky et al., 2019; Rothschild et al., 2018; Smith et al., 2015). For example, short-term changes in diet can rapidly alter bacterial abundances in humans, primates and carnivores (Amato et al., 2015; David et al., 2014; Williams et al., 2013). Moreover, primates living in degraded habitats have less diverse microbiomes (Amato et al., 2013; Barelli et al., 2015), and habitat heterogeneity alters microbiome compositions in elephants and baboons (Chiyo et al., 2014; Grieneisen et al., 2017). Because group members share the same habitat and similar diets, distinct gut microbiota might reflect differences in food availability or habitat type between groups' home ranges

(Amato et al., 2013; Grieneisen et al., 2019). In species with overlapping home ranges, neighbouring groups might therefore share more similar microbiomes than groups living in different or distant areas. However, the relative importance of environmental or social factors is still debated, with some studies suggesting environmental factors as main contributors to microbiome convergence between co-residing conspecifics (Degnan et al., 2012b; Grieneisen et al., 2019), whereas others propose social interactions to have a stronger impact (Goodfellow et al., 2019; Wikberg et al., 2019).

Study design

Here, we simultaneously examined several potential drivers of between-group variation in gut microbial compositions in a wild population of Verreaux's sifakas (*Propithecus verreauxi)*. Two previous studies of this species indicated that group membership is reflected in individuals' gut microbiome compositions (Perofsky et al., 2017; Springer et al., 2017). Springer et al. (2017) investigated, next to the impact of group membership, effects of seasonal variation in diet and the effects of intrinsic factors on microbial composition and diversity in the same study population. They found a clear pattern of seasonal variation, especially on the Firmicutes-Bacteroidetes ratio, while there were no or only weak influences of sex, age class and female reproductive stage. Perofsky et al. (2017) provided a snapshot perspective on the gut microbiomes of a different sifaka population and examined impacts of grooming networks, diet, habitat overlap and host intrinsic factors on microbial similarity and within-host diversity. They found no effect of diet, habitat overlap, kinship or within-group social interactions on microbial similarity but found positive links between age and grooming interactions with microbiome diversity.

To better understand the relative importance of environmental, intrinsic and social factors that drive gut microbial convergence among group members, we set out this study to examine the effects of social interactions, maternal relatedness, diet, habitat structure, habitat overlap and seasonality. We repeatedly collected and analysed faecal samples of up to 41 individuals from 7 different groups during the early and late dry season in two subsequent years. Additionally, we describe Verreaux's sifakas' core gut microbiota. The core microbiota includes only those taxa that are present in the majority of analysed hosts (Hamady & Knight 2009) and is thought to be involved in the gut microbiomes' general functions (Shade & Handelsman 2012). Thus, we contribute an independent observation to the few comprehensive and longitudinal studies of the determinants of the gut microbiome in wild animals.

We expected to find distinct gut microbial communities per group for each field season (Perofsky et al., 2017; Springer et al., 2017). Moreover, within groups, animals that spent more time in body contact, including grooming, were expected to share more similar microbial communities with each other than with other group members (Tung et al., 2015). Maternally related animals should share more similar gut microbiomes with each other than with unrelated individuals, even though the effects might be weak (Amato et al., 2017a; Degnan et al., 2012b; Grieneisen et al., 2017). In addition, we predicted neighbours

and groups inhabiting more similar habitats and those sharing more similar diets, to exhibit greater microbial similarity. Besides, we expected larger groups to exhibit a greater microbiome diversity, but only if members of larger groups engage in more intimate social interactions. Finally, as indicated by a previous study in the same population (Springer et al., 2017), seasonal variation in diet, especially in terms of relative fruit and leave intake, should alter gut bacterial compositions and diversity should be greater during the late dry season as response to an increased fibre intake.

Material & Methods

Study site

This study was carried out in Kirindy Forest, Western Madagascar (44°39'E, 20°03'S). The study area is managed by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF) and belongs to a research station operated by the German Primate Center. Kirindy Forest is a dry deciduous forest and subject to pronounced seasonality, with a short hot, wet season (November to March) and a long dry season (April to October) (Kappeler and Fichtel, 2012).

Study species

Verreaux's sifakas are diurnal, frugi-folivorous and arboreal lemurs endemic to Madagascar. They live in multi-male multi-female groups with group sizes ranging between 2 and 12 individuals in our study population (Kappeler and Fichtel, 2012). Their home ranges are stable over years and partially overlap with those of neighbouring groups, yet, they include core areas of exclusive use (Benadi et al., 2008; Koch et al., 2016a). Additionally, in contrast to anthropoid primates, sifakas groom each other orally rather than manually, which may enhance the possibility for bacterial transmission between individuals. All animals are habituated to observers and individually marked. One of the groups, group M, only entered the study area by the end of 2016, so that data for this group were only available for study year 2017.

Home range features

Forest inventories of 10 randomly selected square plots (~25 x 25m; only 6 plots for group F1) within the home ranges of each group were conducted in 2012 (Koch et al., 2017) and 2016 (Rudolph et al., 2019). We identified all trees with diameters at breast height larger than 5cm, resulting in a data set comprising 12,177 trees of 168 different species found in 66 phenology plots (for details see Rudolph *et al.* 2019).

Behavioural observations

Between April 2016 and March 2018, we conducted focal animal sampling on all adults and juveniles (age > 9 months). Observations lasted 1 h per individual and were conducted for 3 h in the morning and 3 h in the afternoon in an alternating order. We continuously recorded social behaviours (i.e. allogrooming, play, body contact, proximity of <1m, aggression), including the identity of involved conspecific(s), and non-social behaviours, like feeding, locomoting, resting, self-scratching and auto-grooming. We

additionally recorded the identity of feeding plants and parts. As our study involved focal animal observations, it was not possible to record data blind.

Home range overlap

In a previous study (Rudolph et al., 2019), we assed home range sizes of each group with GPS collars (e-obs, Grünwald, Germany) by equipping one male per group during annual captures (for details on capture procedures see Kappeler and Fichtel 2012). On average, we recorded GPS data for 651 days with a mean of 21400 GPS locations per group. To estimate home range overlap among groups for each of the four field seasons, we used the function *kerneloverlaphr* of the *adehabitatHR* package (Calenge, 2006) in R (R Version 3.6.1, R Core Team, 2018). Figure S1 illustrates home range overlaps among groups.

Bacterial gut microbiome analyses

We collected and analysed 519 faecal samples during four field seasons (12.7 ± 3.6 (mean ± SD) total samples per animal; Ø 3.9 samples per animal per season), covering the early dry season (April-May 2016/17) and the late dry season (September-October 2016/17) twice. Samples were only collected when they could be distinctively assigned to an individual. We stored samples in 2 ml polypropylene tubes containing 1 ml RNA*later* (Thermo Fisher Scientific, Waltham, MA, USA) at ambient temperature for 24h. Afterwards, samples were stored at -20°C and shipped to Germany, where further analyses ensued.

Extraction of DNA, amplification, and sequencing of 16S rRNA genes

We extracted DNA from approximately 100 mg of faecal samples using the PowerSoil DNA isolation kit (MoBio, Carlsbad, USA) following the instructions of the manufacturer. However, to ensure complete homogenization of the faecal samples, cells were mechanically disrupted with a FastPrep-24 Classic Grinder (MP Biomedicals, Santa Ana, California, USA). Samples were homogenized for 20 s at 6.5 m/s. Bacterial 16S rRNA gene amplicons were generated using the forward and reverse primers S-D-Bact-0341-b-S-17 (5′- CCTACGGGNGGCWGCAG-3′) and S-D-Bact-0785-a-A-21 (5′-GACTACHVGGGTATCTAATCC-3′) (Klindworth et al., 2013), including the Illumina MiSeq sequencing adaptors and target the V3 to V4 variable regions of the 16S rRNA gene. PCR reaction mixtures (total volume 50 µl) contained 1 U Phusion high fidelity DNA polymerase (Biozym Scientific, Oldendorf, Germany), 2.5 µl DMSO (5%), 1 µl of forward and reverse 16S rRNA gene primers (10 µM), 1 µl dNTP (10 mM), 0.2 µl $MgCl_2$ (50 mM), and 25 ng of isolated DNA. Thermal cycling conditions were as follows: initial denaturation for 1 min at 98 °C, 25 cycles at 98 °C for 45 s, 55 °C for 45 s, and 72 °C for 30 s, and a final extension at 72 °C for 5 min. We included negative controls (without template) and positive controls (with genomic E. coli DH5α DNA) in all PCRs. We used agarose gel electrophoresis to verify correct amplicon size (~550 bp). PCR reactions were performed in triplicates for each sample, then pooled in equimolar amounts and purified using MagSi-NGS^{PREP} Plus (Steinbrenner, Wiesenbach, Germany) as described by the supplier. Nextera DNA Library

Prep kits were used for indexing PCR products according to the manufacturer's manual (Illumina), followed by dual-indexed paired-end sequencing with the Illumina MiSeq platform (2 x 300 bp) and v3 chemistry (Illumina, San Diego, CA, USA).

Bioinformatic processing of 16S rRNA gene amplicon sequences

Paired-end sequencing data from the Illumina MiSeq were quality-filtered with fastp (v0.19.4) (S. Chen et al., 2018) using default settings with the addition of an increased per base phred score of 20, base pair corrections by overlap (-c), as well as 5′- and 3′-end read trimming with a sliding window of 4, a mean quality of 20 and minimum sequence size of 50 bp. After quality control, the paired-end reads were merged using PEAR (v0.9.11) (Zhang et al., 2014) and primers clipped using cutadapt (v1.18) (Martin, 2011) with default settings. Sequences were then processed using VSEARCH (v2.9.1) (Edgar, 2010). Processing included sorting and size-filtering of the paired reads to ≥300 bp (--sortbylength --minseqlength 300) and dereplication (--derep_fulllength). Dereplicated amplicon sequence variants (ASVs) were denoised with UNOISE3 using default settings (--cluster_unoise –minsize 8) and chimeras were removed (--uchime3_denovo). An additional reference-based chimera removal was performed (--uchime_ref) against the SILVA SSU NR database (v132) (Quast et al., 2013). Raw reads were mapped to ASVs (--usearch_global–id 0.97). Finally, we taxonomically classified ASVs with BLAST 2.7.1+ (Altschul et al., 1990) against the SILVA SSU v132 database and removed chloroplasts and extrinsic domains from the data set.

The following analyses were performed on data normalised with the GMPR method (v0.1.3) (L. Chen et al., 2018) and conducted in R (R v3.6.1, R Core Team, 2018). To assess alpha diversity, i.e. the bacterial diversity within samples, we calculated Faith's Phylogenetic Diversities (PD) (Faith, 1992) with the *picante* package (v1.8) to assess microbial phylogenetic representation, and Shannon's indices (Shannon, 1948) to examine community evenness, with the *diversity* function of the *vegan* package (v2.5-6) (Oksanen *et al.* 2016). For examinations of beta diversity, i.e. variance in community composition among samples, we computed two measures: Bray-Curtis dissimilarities and generalized UniFrac distances (GUniFrac). Bray-Curtis dissimilarities detect differences in microbial abundances, which we calculated with the *vegdist* function of the *vegan* package. GUniFrac distances also detect microbial abundances but further include information on counts and adjusted weights of phylogenetic branch lengths (Chen et al., 2012). We computed GUniFrac distances with the *GUniFrac* function of the *GUniFrac* package (version 1.1) (Chen et al., 2012). Core gut microbiota were determined following definitions of prior studies, i.e. ASVs present in ≥ 90% of samples were categorized as core ASVs (Ainsworth et al., 2015; Grieneisen et al., 2017; Li et al., 2013).

Group differences in ASV-based community composition were visualised with nonmetric multidimensional scaling (NMDS) ordinations based on GUniFrac and Bray-Curtis distance matrices.

Additionally, we built heat trees to illustrate and examine variations in microbiome phylotypes between groups with the metacoder package (Foster et al., 2017). Heatmaps were built with the *ampvis2* package (version 2.5.5) (Skytte et al., 2018).

Statistical analyses

All statistical analyses were conducted in R.

Mantel tests - Beta diversity and group membership

We examined the relationship between group membership and beta diversity with Mantel tests using 1,000 permutations, including the original data as one permutation. We conducted four Mantel tests, each including only samples of one of the four field trips. Animal ID was assigned to the samples to control for repeated measures. The test statistic yielded the mean absolute differences in dissimilarities within and between groups. We determined p-values as the proportion of permutations that resulted in larger test statistics than or equal to the test statistics of the original data. The unpublished functions for this analysis were kindly provided by Roger Mundry.

GLMM - Beta diversity within groups

To investigate whether samples from the same individual are more similar than samples between group members, we computed a generalized linear mixed model (GLMM) (Baayen et al., 2008) from the *lme4* package (version: 1.1.21) (Bates et al., 2012) with the optimizer "bobyqa". Mean GUniFrac distances per ID dyad and field season were used as response, the factor "same individual" (yes or no) was used as predictor, individual dyads and group ID were used as random effects and field season as random slope. To control for seasonal variation, we included field season as fixed effect. We included random slopes to keep type I error rates at the nominal level of 5% (Barr et al., 2013). P-values for individual effects were based on likelihood ratio tests comparing the full with the respective null models using the *drop1* function (Barr et al., 2013). In this and all following GLMMs, we controlled for assumptions of normal distributions, homoscedasticity and collinearity, and we checked for model stability. Comparisons between full and null or reduced models were done with likelihood ratio tests (R function ANOVA with argument test set to "Chisq") (Dobson, 2002; Forstmeier and Schielzeth, 2011). Null models contained only intercepts, random effects and random slopes; reduced models additionally contained assigned control factors. We obtained effect sizes of the full models for the entirety of fixed and random effects with the function *r.squaredGLMM* of the package *MuMIn* (version 1.43.6) (Barton, 2018). Confidence intervals were assessed with parametric bootstrapping using an adjusted *bootMer* function from the *lme4* package. Roger Mundry also kindly provided this adjusted function.

GLMM - Beta diversity and body contact within groups

We examined whether group members that spent more time in body contact, including grooming and activities (i.e. feeding, resting) in body contact, share more similar microbiome communities. Behavioural data for this analysis were collected from January to May 2017 and June to October 2016/17, i.e. covering the time of three out of four field seasons plus the 3 months prior to the respective field seasons (i.e. data for the field season April-May 2016 were not included in this analysis as there were no behavioural observations conducted from January to March 2016). Observations of juveniles usually start in the first April after their birth, when they are about 9 months old. Hence, to ensure a balanced data set, juveniles were excluded from the early dry season 2017, as there were no observations between January and March for these animals. During this time, we collected 1,364 h of behavioural data of which Verreaux's sifakas spent on average 3.6 ± 1.6 min/h (mean ± SD) in body contact. We computed a GLMM with the mean GUniFrac dissimilarities of individual dyads per field season as response and mean time spent in body contact (in min/h) as predictor. Individual dyads and group ID were used as random effects and field seasons as random slopes. To control for effects of field season and maternal relatedness (see below), we included both factors as fixed effects.

GLMM - Beta diversity and maternal relatedness

We investigated the potential effect of genetic maternal relatedness on gut microbiome similarity among individuals. Maternal relatedness of older individuals was determined via genetic analyses in a prior study (1995 – 2005, Kappeler & Schäffler 2007). For younger individuals, we used behavioural observations of mother-offspring dyads to determine relatedness (Kappeler and Fichtel, 2012). For 9 out of 41 individuals, mothers could not be assigned as they were absent during genetic data collection or adult individuals immigrated into the study population after 2005. These individuals were excluded from the analysis. We considered animals as maternally related if they were known to have one of the following degrees of kinship: mother-offspring, siblings or half-siblings, grandmother-grandchild, aunt/uncle-nephew/niece.

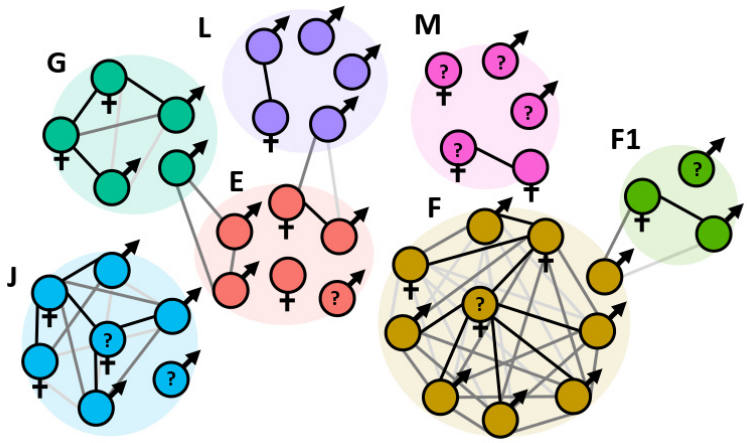


Figure 1 Group compositions and maternal relatedness within the study population. Circles represent individuals and indicate sex. Circles containing question marks indicate missing information on the respective animals' mothers. Lines indicate degrees of maternal relatedness. Black lines indicate mother-offspring dyads, dark grey lines indicate siblings and light grey lines indicate grandmother-grandchild or aunt/uncle - nephew/niece dyads.

Figure 1 illustrates all known degrees of maternal relatedness within the study population. For statistical analysis, we computed a GLMM in the same manner as described above. Mean GUniFrac distances of individual dyads per field season were used as response, relatedness (yes or no) and the interaction between relatedness and group membership (yes or no) were used as predictors, individual dyad as random effect and field season as random slope. To control for effects of group ID and field season on GUniFrac distances, we included both factors as fixed effect.

Pearson's correlation - Beta diversity and home range dissimilarities among groups

We examined whether groups with ecologically more similar home ranges share more similar gut microbiomes. To estimate differences in home ranges, we computed Bray-Curtis dissimilarities among groups based on tree species abundances within each groups' home range. Next, we averaged GUniFrac distances for each group dyad from all samples. We then calculated a Pearson's correlation, examining the link between dyadic GUniFrac distances and dyadic habitat dissimilarity between groups ($n_{Group\ dyads}$ = 21).

GLMM - Beta diversity and home range overlaps between groups

We investigated whether neighbouring groups with overlapping home ranges share more similar microbiomes than groups with non-overlapping home ranges with a GLMM. Mean GUniFrac distances per group dyad per field season were used as response, mean home range overlaps per field season were used as predictors, group dyad was used as random effect and field season as random slope. To control for seasonal variation in ranging patterns (see Rudolph et al., 2019), we included field season as fixed effect.

GLMM - Beta diversity and diet dissimilarity between groups

Next, we examined whether groups with more similar diets share more similar gut microbiomes. To estimate differences in diets, we computed Bray-Curtis dissimilarities between groups based on proportions of feeding times spent on different plant species per field season. Data collection on feeding behaviour for this analysis was conducted from March to May 2017 and August to October 2016/17, resulting in a total of 280 h of feeding data. For the first field season (March to May 2016) no data on consumed plant species were recorded, which is why this analysis was only performed for the three remaining field seasons. We averaged GUniFrac distances and diet dissimilarities per group dyad per field season. For statistical analysis, we computed a GLMM in the same manner as described above. GUniFrac distances were used as response, mean diet dissimilarity as predictor, group dyad was used as random effect and field season and diet dissimilarity as random slopes. To control for seasonal variation in GUniFrac distances, we included field season as fixed effect. Moreover, we compared fruit and leave

intake rates between groups and seasons in additional GLMMs described in the supplementary materials (Appendix Chapter 4).

GLMM - Alpha diversity

We applied three GLMMs to examine effects of study year (2016 and 2017), season (early dry – late dry), group ID, group size, mean fruit and leave intake per season per animal and mean body contact rates per season per animal microbiome diversity. Phylogenetic diversity (PD) per sample was the response in all models. In the first model, study year, season, group ID and mean proportions of consumed fruits and leaves per field season were predictors, sex was a control factor, animal and group ID were random effects and season (early dry – late dry), fruit and leave intake and study year were used as random slopes. In the second model, group size was included as predictor, study year and sex were control factors, group and animal ID were random effects and group size and study year were random slopes. In the third model, we examined effects of time spent in body contact with group members via affiliative interactions (i.e. grooming, resting and feeding in contact). We used the mean time spent in body contact per field season as predictor, study year and sex as control factors, group and animal ID as random effects and body contact and study year as random slopes.

All analyses were additionally conducted with Bray-Curtis dissimilarities for beta diversity and Shannon indices for alpha diversity (Appendix Chapter 4).

Seasonal variation in relative abundances of phyla

We examined seasonal effects on microbiome composition by assessing changes in individual mean monthly abundances of core phyla within each of the two study years. We conducted Kruskal-Wallis tests, as data violated assumptions for parametric analyses, and carried out post hoc comparisons with Dunn's tests (Bonferroni correction) using the package FSA (version 0.8.22).

Social network statistics – Comparisons with Perofsky et al. (2017)

To better compare the effects of social interactions on gut microbiomes in our study population with the findings in a different population, we replicated some of the analyses from Perofsky et al. (2017). More precisely, we also constructed social networks based on grooming interactions and did so for each of three field seasons based on the data set described above. However, in contrast to Perofsky et al. (2017), not all study animals were connected to their group members in our grooming networks (Figure S6). Compared to other primates, sifakas devote little time to grooming interactions (Richard, 1985) and while grooming bouts occur frequently and on a daily basis, they usually remain short (Lewis, 2010). In our study, animals spent on average 18s ± 10s per hour (mean ± SD) grooming. Most likely, our data did not detect all existing connections and we had to exclude unconnected individuals from the data set to run network statistics. Due to the missing data, there is limited scope for interpreting our results.

Nevertheless, we provide details on methods and results and a brief discussion of grooming network analyses in the appendix of this chapter.

Results

519 faecal samples of 41 different individuals contained 5,995 bacterial ASVs and high quality 21,596,631 amplicon sequences. 2,966 of all ASVs could be taxonomically assigned and belonged to 12 phyla: *Firmicutes* (1,442), *Bacteroidetes* (927), *Proteobacteria* (174), *Actinobacteria* (155), *Cyanobacteria* (134), *Verrucomicrobia* (57), *Synergistetes* (43), *Fibrobacteres* (17), *Spirochaetes* (9), *Tenericutes* (4), *Epsilonbacteraeota* (3) and *Armatimonadetes* (1). About 50% of all reads belonged to the 5 most common families: *Prevotellaceae* (17%), *Lachnospiraceae* (15%), *Ruminococcaceae* (7%), *Rikenellaceae* (6%) and *Acidaminococcaceae* (5%) (Figure 2a).

The core gut microbiota of Verreaux's sifakas

The ASVs defined as core microbiome occurred in 96.4% ± 3.2% (mean ± SD) of all samples and in 95.9% ± 3.7% of all individuals (controlling for repeated sampling). The core comprised 214 ASVs of which 47 could not be assigned to any taxonomy. The remaining 167 ASVs belonged to eight different phyla: *Firmicutes* (119), *Actinobacteria* (13), *Proteobacteria* (12), *Bacterioidetes* (8), *Synergistetes* (5), *Cyanobacteria* (4), *Fibrobacteres* (3) and *Verrucomicrobia* (3). In the core microbiome, 50% of all reads belonged to the 5 most common families: *Lachnospiraceae* (21%), *Rikenellaceae* (11%), *Acidaminococcaceae* (7%), *Ruminococcaceae* (6%) and *Puniceicoccaceae* (6%) (Figure 2b).

Beta diversity (GUniFrac)

Effects of host and group membership

Samples from the same individuals were more similar than samples between group members (GLMM: χ^2 = 26.366, df = 1, $p < 0.001$, $R^2_{m/c}$ = 0.14/0.88) (Table S1, Figure S2). Group membership impacted the gut microbiome as samples of group members were more similar to each other than samples from individuals living in different groups (Figure 3 and S3). This was true for each field season (Table 1). All groups exhibit very similar microbial compositions up to the family level and differences between groups appear mainly on the genus level and beyond. In more detail, groups seem to mainly differ within genera of the more

Table 1 Results of Mantel tests comparing GUniFrac distances between seven groups of Verreaux's sifakas.

Season	$n_{samples}$	$n_{individuals}$	$\bar{x}_{same\ group}$	$\bar{x}_{different\ group}$	*P*
early dry 2016	92	29	0.121	0.155	**<0.001**
late dry 2016	116	29	0.119	0.154	**<0.001**
early dry 2017	155	39	0.125	0.147	**<0.001**
late dry 2017	156	36	0.110	0.148	**<0.001**

abundant phyla, i.e. *Firmicutes*, *Bacterioidetes*, *Actinobacteria*, *Cyanobacteria*, *Verrucomicrobia* and *Fibrobacteres* (Figure 4). Moreover, heatmaps of the most common genera indicate noticeable variation between groups in terms of abundance and presence of unclassified ASVs (Figure 5).

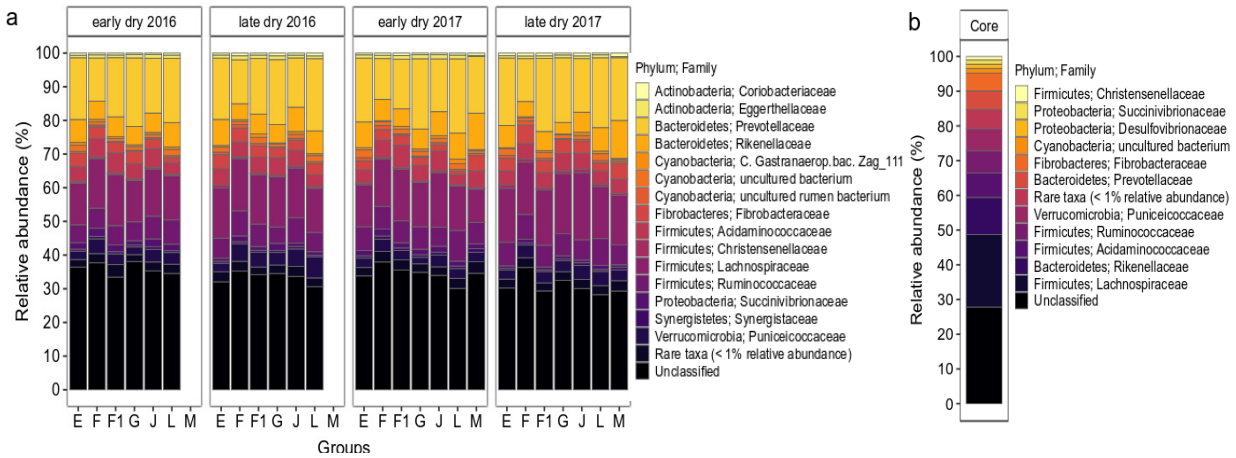


Figure 2 Relative abundances of a) all microbial families and b) core families. Data comprise 519 faecal samples of seven groups of wild Verreaux's sifakas during four field seasons.

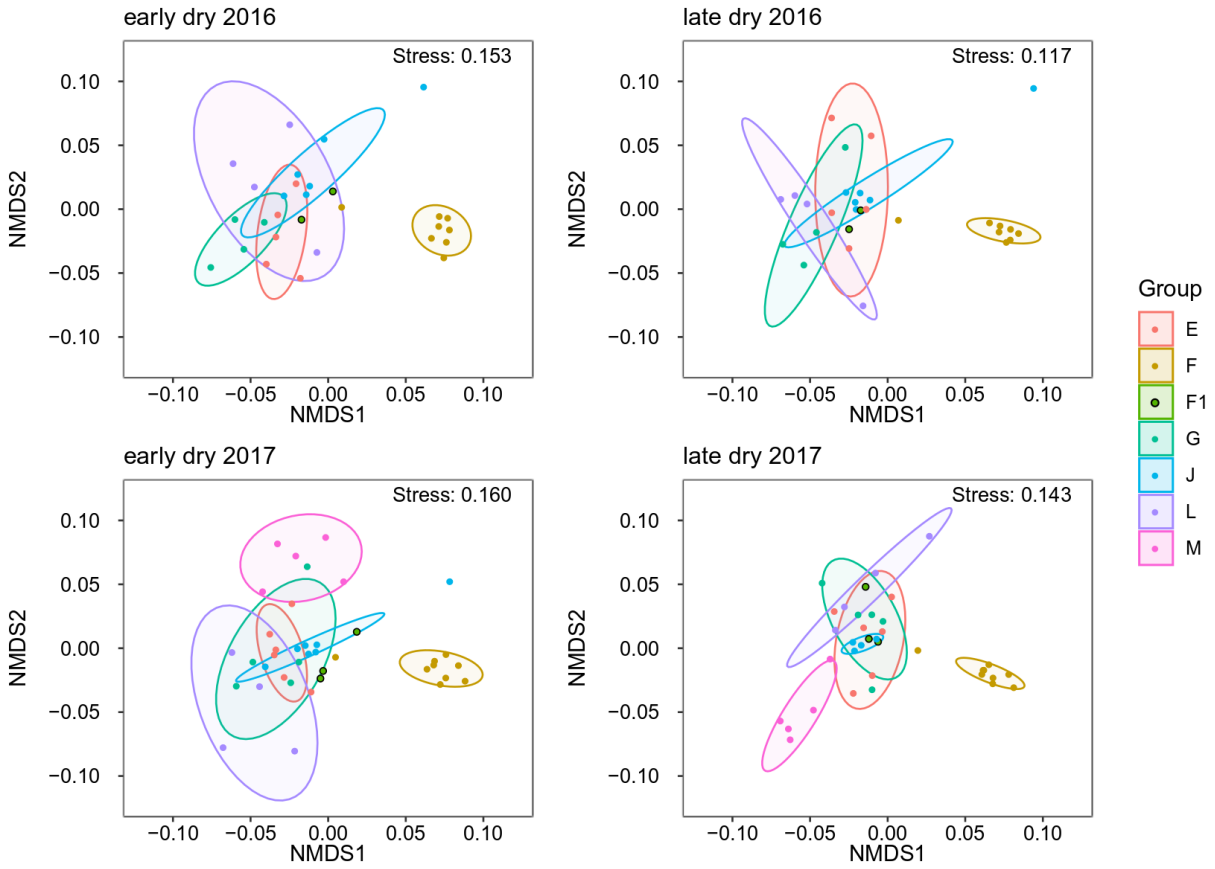


Figure 3 Nonmetric multidimensional scaling (NMDS) ordination of Verreaux's sifakas' gut bacterial composition data (GUniFrac distances) for each of the four field seasons. Data points represent individuals and colours indicate group membership. Ellipses indicate the 80% confidence ellipse for each group. For group F1, there were not enough data points to create ellipses, so we outlined the data points for better visibility. Several samples per individual per season were collected, however, here we only plotted one data point per animal, based on average dyadic beta dissimilarity per field season, to facilitate the overview.

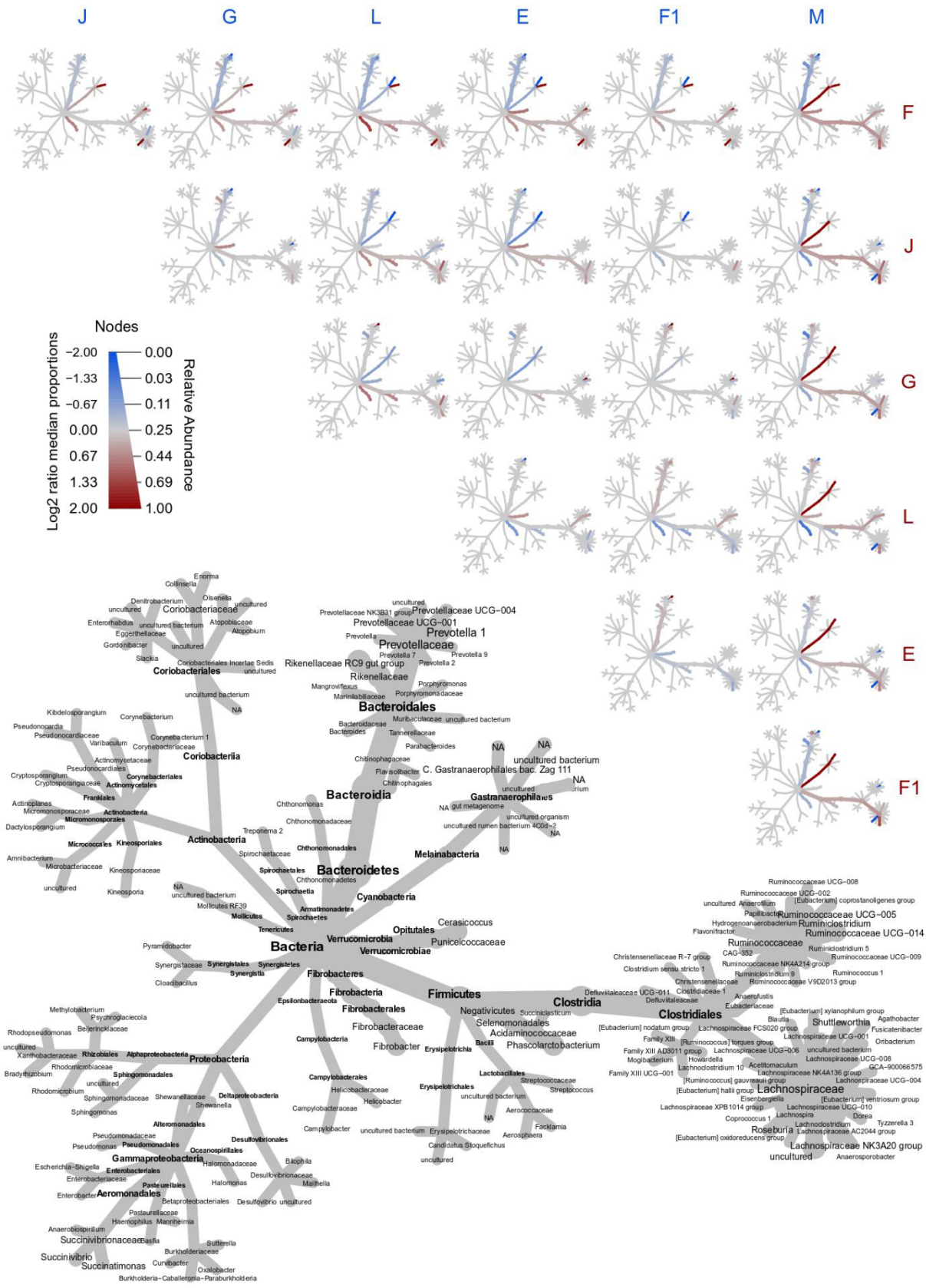


Figure 4 Differential heat tree matrix depicting between-group variation in gut microbial communities up to the genus level. The size of individual nodes within the grey cladogram depicts relative abundances of taxa identified at that taxonomic level. Smaller cladograms show pairwise comparisons between groups, based on Wilcoxon-signed rank tests: blue nodes indicate significantly higher abundances of the respective taxon in the group stated on the abscissa, than in the group stated on the ordinate. Red nodes indicate the opposite.

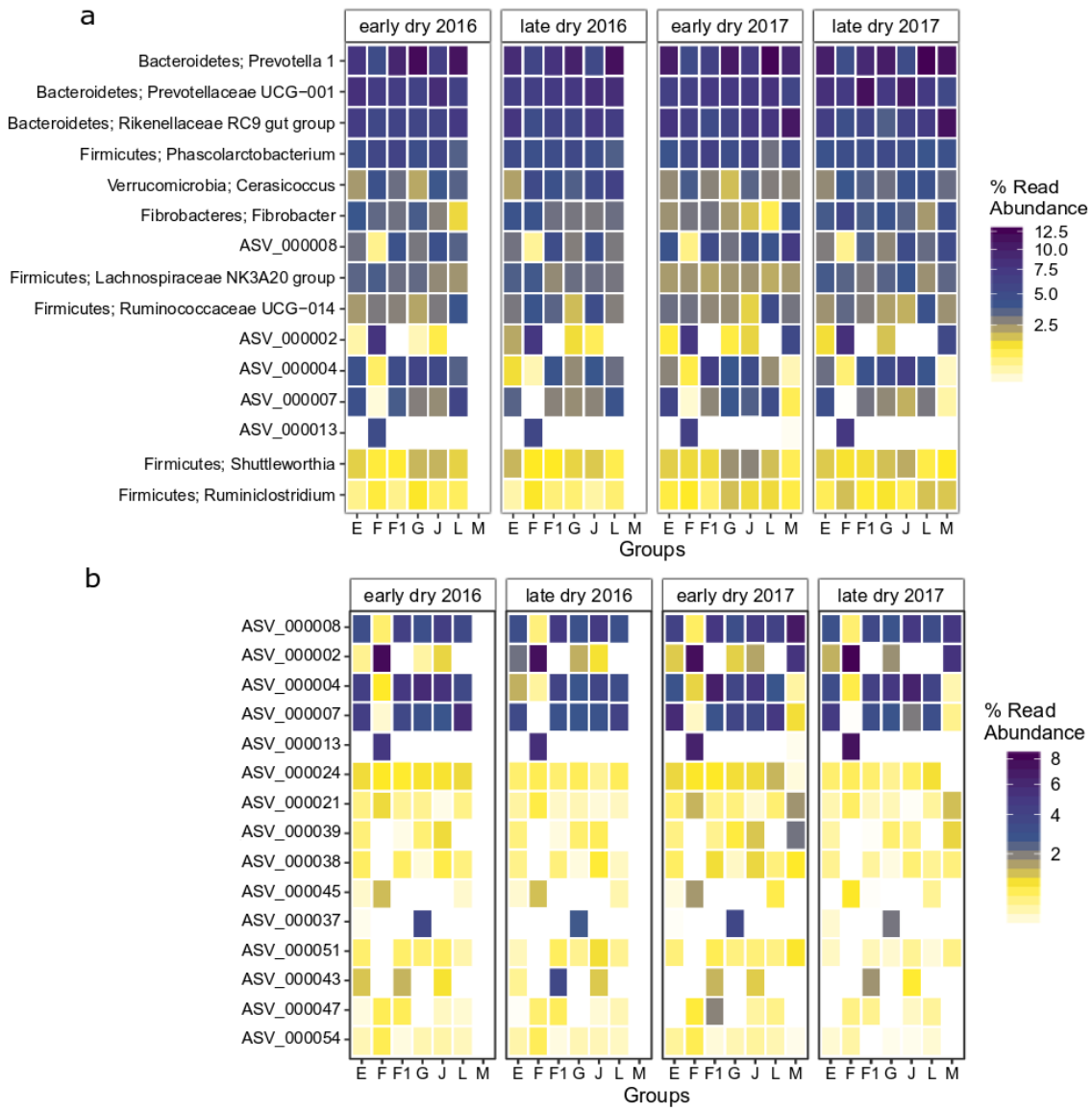


Figure 5 Heatmaps of the 15 most abundant a) genera and b) unassigned ASVs in Verreaux's sifakas' gut microbiomes

Effects of body contact within groups

The model examining effects of the time group members spent in body contact on dyadic GUniFrac dissimilarity was not significant (χ^2 = 0.223, df = 1, p = 0.637, $R^2_{m/c}$ = 0.52/0.61) (Table S2, Figure 6 a).

Effects of maternal relatedness

The model examining the effects of maternal relatedness on GUniFrac distances between individuals was highly significant (χ^2 = 164.418, df = 2, p < 0.001, $R^2_{m/c}$ = 0.56/0.91) (Table S3). Maternal relatives share more similar microbiomes and there was a tendency for relatives living in the same group to share more similar microbiomes than relatives living in different groups (test of the interaction between maternal relatedness and group membership: χ^2= 3.679, df = 1, p = 0.055). Within groups, relatives shared more similar microbiomes than unrelated group members (Figure 7).

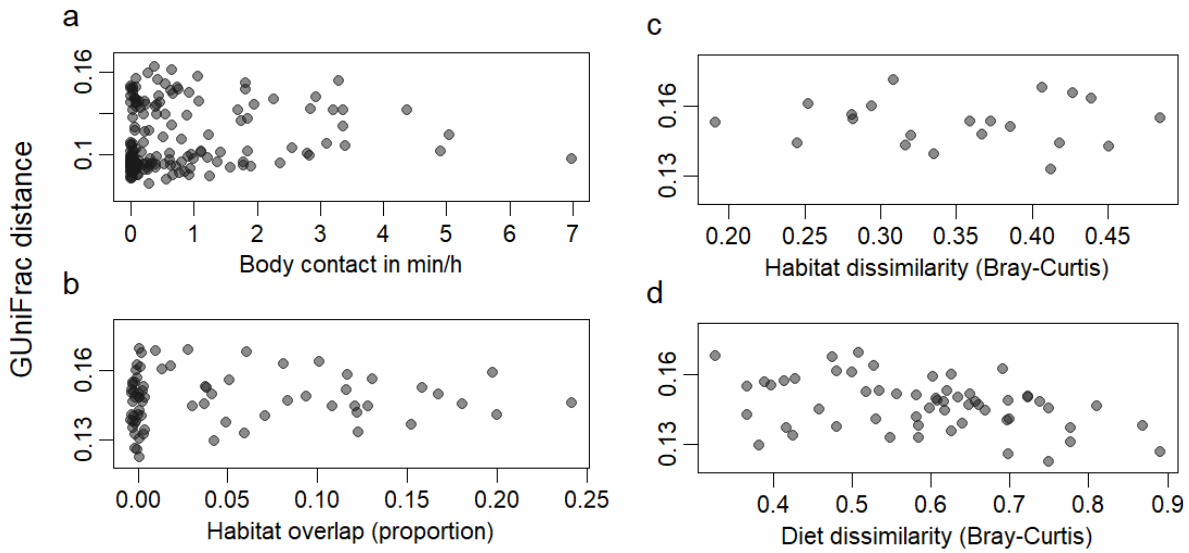


Figure 6 Influence of social contact within groups and differences in habitats and diets between groups on GUniFrac distances. a) Data points depict mean body contact rates per dyad per field season; b + d) Data points depict mean habitat overlaps and mean diet dissimilarities of group dyads per field season. c) Data points depict habitat dissimilarities of group dyads

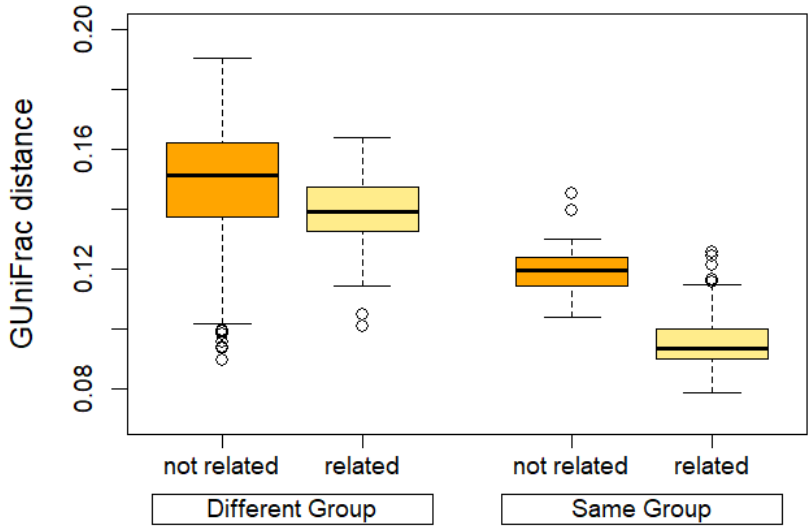


Figure 7 Influence of maternal relatedness on GUniFrac distances between individuals. Boxplots comprise dyads of all individuals with known maternal relationships. Lines indicating median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers

<u>Effects of habitat dissimilarity, habitat overlap and diet dissimilarity between groups</u>

Habitat dissimilarity and GUniFrac distances between groups were not correlated (Pearson: r = -0.043, $n_{Group\ dyads}$ = 21, p = 0.852) (Figure 6c). The models examining effects of habitat overlap and diet dissimilarities on groups' GUniFrac distances were not significant either (habitat overlap: χ^2 = 0.286, df = 1, p = 0.596, $R^2_{m/c}$ = 0.11/0.95; diet dissimilarity: χ^2 = 0.399, df = 1, p = 0.528, $R^2_{m/c}$ = 0.09/0.95) (Tables S4 & S5, Figure 6b & d).

Alpha diversity (PD)

Effects of group membership, season, study year and diet

The model examining effects of group membership, season (early dry vs. late dry), study year and diet on individual PDs was significant (χ^2 = 113.650, df = 10, p < 0.001, $R^2_{m/c}$ = 0.31/0.38) (Table S6). In detail, group membership and study year affected individual alpha diversity. Members of group M had lower PDs than all groups except for group J. Group J had lower PDs than groups F, G and L (Table S7, Figure 8a). In 2017, all animals had lower PDs than in 2016 (Figure 8b). During the late dry season, PDs were slightly higher, while no correlations were found with individuals' fruit and leave intake rates (Figure 8c, d & e).

Effects of group size

The second model, examining effects of group size on PDs was not significant (χ^2 = 0.298, df = 1, p = 0.858, $R^2_{m/c}$ = 0.17/0.41) (Table S8) (Figure 8 f). Body contact rates were not correlated to group size either (Pearson: r = -0.078, n_{ID} = 41, p = 0.627).

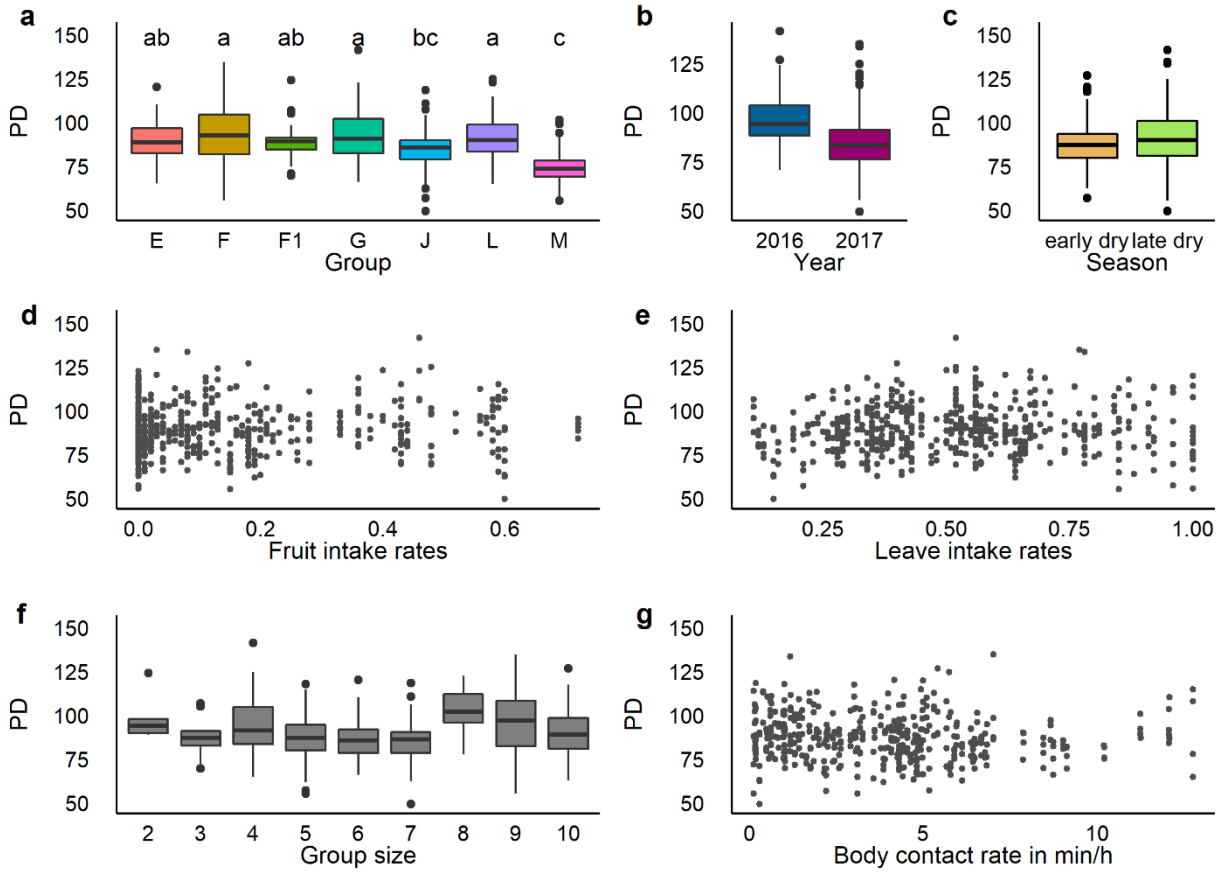


Figure 8 Influence of various factors on alpha diversity (Phylogenetic diversity). Coloured graphs indicate significant effects. a, b & c) Influence of group identity, study year and season. Boxplots comprise all collected samples with lines indicate median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers. d & e) Influence of mean fruit and leave intake rates per field season. f) Influence of mean group size per field season. g) Influence of mean time spent in body contact per field season

Effects of body contact within groups

The model examining effects of time spent in body contact within groups was not significant (χ^2 = 1.702, df = 1, p = 0.192, $R^2_{m/c}$ = 0.11/0.29) (Table S9, Figure 8g).

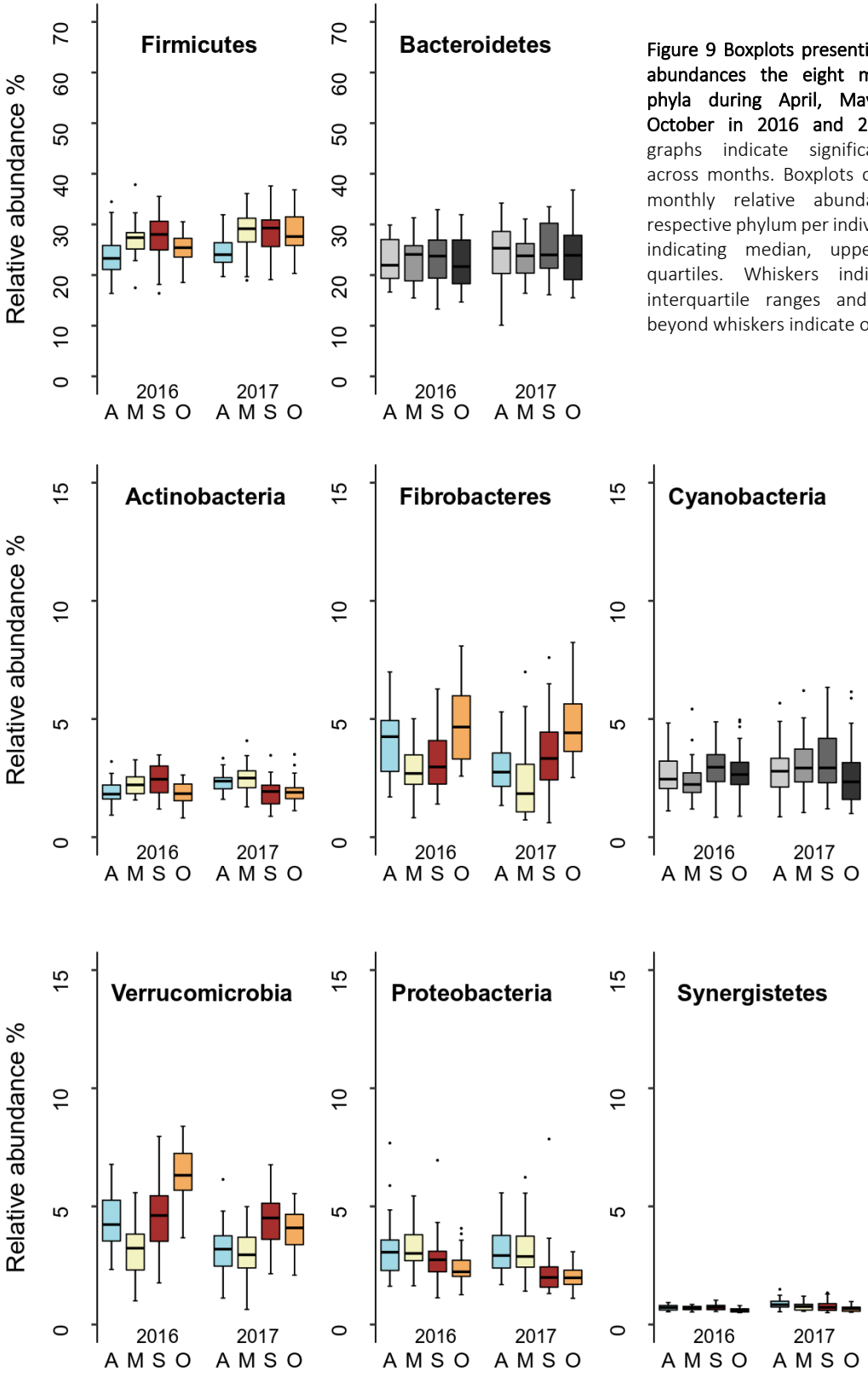


Figure 9 Boxplots presenting the relative abundances the eight most abundant phyla during April, May, September, October in 2016 and 2017. Coloured graphs indicate significant variations across months. Boxplots comprise mean monthly relative abundances of the respective phylum per individual with lines indicating median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers

Seasonal variation in relative abundances of core phyla

We detected significant variations of monthly relative abundances in six out of eight core phyla in both study years (Tables S10 & S11). The phyla *Bacteroidetes* and *Cyanobacteria* did not change in relative abundances with progressing dry season. Abundances of *Firmicutes*, *Fibrobacteres* and *Verrumicrobia* were significantly lower during the early dry season, while *Proteobacteria* showed opposite patterns (Figure 9). However, some of these effects varied with study year and were often more pronounced in 2017.

Discussion

We examined drivers of between-group variation in gut microbial communities of seven wild Verreaux's sifaka groups. Throughout all field seasons there was a consistent effect of group membership, as groups differed in both, composition and diversity of their gut microbiomes. Within groups, social contact neither predicted microbiome compositions nor bacterial diversity. Maternally related individuals shared more similar microbiomes, however, unrelated group members had more similar microbiomes than relatives living in different groups, indicating that the effects of group membership are stronger than the effects of kinship. None of the environmental predictors, i.e. habitat overlap, habitat dissimilarity and diet dissimilarity, explained variation of between-group gut microbiomes. Altogether, we conclude that environmental factors may determine the general arrangement for species- and population-specific gut microbial communities, whereas finer-scaled environmental differences between local groups might not have detectable effects. In contrast to most of the primate literature, we found kinship to play an important role for within-group microbial homogeneity. Moreover, social contact did not predict similarities in gut microbiomes within groups. Nevertheless, rare physical contact between individuals of different groups and frequent physical contact among group members remains a likely contributor to the here found group membership effects, however, more research is required to confirm this assumption.

Sociality may drive variation in microbiome communities between but not within groups

As expected, group membership predicted microbiome composition and diversity in our study species, confirming results of prior studies (Perofsky et al., 2017; Springer et al., 2017). In Verreaux's sifakas, group members regularly engage in grooming bouts and, like many lemur species (Eppley et al., 2017b; Morland, 1993; Ostner, 2002; Pereira et al., 1999), they use social thermoregulation, i.e. resting in body contact with conspecifics, especially during cold nights. In contrast, contact among individuals between groups is rare and most intergroup encounters proceed without any physical interactions (Benadi et al., 2008; Koch et al., 2016b). Therefore, increased physical contact among group members is a likely driver for greater within-group similarities in gut microbiomes.

Within groups, however, variation in body contact between individuals did not further predict microbial similarity. This result contrasts findings of prior studies of chimpanzees and baboons (Moeller et al., 2016; Tung et al., 2015), but confirms findings in sooty mangabeys (Gogarten et al., 2018) and a different population of Verreaux's sifakas (Perofsky et al., 2017). In contrast to non-human primates, sifakas groom orally, which may facilitate bacterial transmission and sharing between individuals (Schmidt et al., 2019). However, on the other hand, Verreaux's sifakas also devote relatively little time to social activities (Richard, 1985) and grooming bouts are fairly short (Lewis, 2010). While proximity and grooming between group members shapes groups' distinct gut microbiomes, the generally low social interaction rates within groups may not further inflict dyadic microbial convergence.

Alpha diversity differed among groups, but this effect was not driven by variation in group size. As individuals in larger groups did not engage more frequently in social interactions either, which might increase social transmission of bacteria (Turnbull et al., 2011), this result is conclusive. In terms of between-group variation in alpha diversity, Grieneisen et al. (2017) propose a link between home range sizes and gut microbial diversity. Larger home ranges may harbour a larger variety of microbes which could, through direct transmission, increase animals' alpha diversity. Yet, differences in groups' home range sizes during the time of data collection, which are reported elsewhere (Rudolph et al., 2019), do not explain variation in alpha diversity in this study. For example, members of group M, which had significantly lower bacterial diversities than most of the other study groups, occupied the largest home range, whereas members of group J had similar bacterial diversities in relation to the other groups despite occupying the smallest home range.

Increased glucocorticoid concentrations (GCs) can result in a loss of microbial diversity and richness, as shown in studies in lab mice and barn swallows (*Hirundo rustica erythrogaster*) (Bailey et al., 2011; Levin et al., 2016). Similarly, parasite infections can alter microbiome composition and diversity (Morton et al., 2015; Zaiss and Harris, 2016). However, our study groups did not differ in GCs or helminth prevalence during the study period (Rudolph et al., 2019), ruling out potential effects of GCs and helminths on group-level alpha diversity. Variation in consumed plant species and differences in habitat features are also likely to alter alpha diversities between groups (Clayton et al., 2018; Reese and Dunn, 2018), yet, here we could not detect any links. Thus, the drivers for between-group variation in bacterial diversities remain unidentified in this study.

Individuals that spent more time in body contact with group members did not harbour more diverse microbiomes. Other studies examining effects of affiliation on alpha diversity reported various patterns. In line with our findings, no correlation was found in baboons (Grieneisen et al., 2017), while negative correlations were reported in red-bellied lemurs (Raulo et al., 2017). Positive correlations were found in chimpanzees, howler monkeys (Amato et al., 2017b; Moeller et al., 2016) and in a different population of Verreaux's sifakas (Perofsky et al., 2017). The findings of Perofsky et al. (2017) are based

on grooming network metrics, whereas we used dyadic interaction rates. After replicating some of the statistical analyses of Perofksy et al. (2017), we concluded that our data are insufficient in density for conducting reliable social network analyses and refrained from inferring meaningful conclusions from these analyses (see Appendix Chapter 4). Thus, it is possible that differences in observation and statistical methods account for the different results found between Perofsky et al. (2017) and our study. However, it may also be that variation in environmental conditions affects animals' social interaction patterns in different populations. Altogether, the impact of social contact on alpha diversity seems to vary within and between species. Differences in social patterns may explain these variations (Kuthyar et al., 2019), yet, more research in more species is required to understand the mechanisms.

Direct physical contact constitutes one important mechanism for microbial transmission. However, there remains a lack of groundwork for identifying the routes and conditions of these transmissions (Brito et al., 2019; Kuthyar et al., 2019; Robinson et al., 2019). The intensity of microbial transmissions could be impacted by the duration of social interactions, but may additionally depend on bacteria's viability under external environmental conditions, for example when exposed to certain temperatures or ultraviolet radiation (Browne et al., 2017; Ferguson and Signoretto, 2011). Less direct pathways can also contribute to microbial transmissions. For example, humans can emit "microbial clouds", i.e. airborne microbes, which may colonize other humans (Meadow et al., 2015) but usually comprise mainly of skin-associated bacteria (Browne et al., 2017). Surfaces that came in contact with human or animal hosts can harbour, amongst others, high proportions of intestinal-associated bacteria which have the potential to transmit to other hosts (Browne et al., 2017; Song et al., 2013). Thus, proximity alone may be sufficient for causing microbial convergence in cohabitating individuals without further ado of direct social contact. Altogether, research on the social transmission of microbes remains in its infancy and more research is necessary to explain the various patterns found across and within taxa.

Maternally related individuals share more similar microbiomes

In line with studies on red squirrels (*Tamiasciurus hudsonicus*), cheetahs (*Acinonyx jubatus*) and gopher tortoises (*Gopherus polyphemus*) (Ren et al., 2017; Wasimuddin et al., 2017; Yuan et al., 2015), maternally related individuals shared more similar microbiomes than maternally unrelated individuals, even after controlling for group membership. This result contrasts with findings in studies of primates, where either no or only weak links with kinship were found (Degnan et al., 2012b; Goodfellow et al., 2019; Grieneisen et al., 2017; Tung et al., 2015). Over a course of a lifetime, social interactions can crucially shape individuals' gut microbiomes (Björk et al., 2019). In species spending large proportions of their times engaging in social activities, like chimpanzees or baboons, majority of microbial communities might thus be acquired via social transmission, potentially replacing maternally inherited phylotypes (Moeller et al., 2016; Ren et al., 2017). In species with fewer social interactions, however, maternal effects on gut

microbiomes might last into adulthood, which would explain our findings. The effects of maternal relatedness on Verreaux's sifakas' microbiomes likely contributed to the effects of group membership, as the majority of maternally related individuals lived within the same group. However, since maternally unrelated group members shared more similar microbiomes than relatives living in different groups, genetic relatedness is clearly not the only driver for between-group variation in microbiome compositions in this species.

Neither habitat nor diet explain between-group variation in microbial communities

Our study site is very heterogenous in terms of forest structure and composition (Kappeler and Fichtel, 2012; Sorg and Rohner, 1996) and sifakas' home ranges differ in both, food tree richness and abundances (Rudolph et al., 2019). However, neither home range similarity nor home range overlap reflected microbiome similarities between groups. For the latter, Perofsky et al. (2017) found similar patterns in another population of Verreaux's sifakas. In contrast, various studies in other primates and fish reported links between variation in habitat type and microbiome composition or diversity (Amato et al., 2015; Barelli et al., 2015; Bennett et al., 2016b; Björk et al., 2019; Greene et al., 2019b; Smith et al., 2015). However, these studies compared groups or populations which either lived in greater distance to each other and/or inhabited highly different landscapes, e.g. disturbed vs. undisturbed forests or lakes vs. streams, whereas we compared neighbouring groups living within an area of $1km^2$ of the same habitat type. Thus, the comparatively minor variations in habitat features between our study groups do not seem to predict microbiome variations.

Groups did not vary in their leave and fruit intakes across seasons (see Appendix Chapter 4), but some groups consumed more similar plant species than others. However, more similar diets did not predict microbiome similarities and the amounts of fruits or leaves in the diet were not related to animals' gut microbial diversity. The latter result is consistent with findings of a prior study in the same population (Springer et al., 2017). Sifakas' gut microbiomes clearly reflect their frugi-folivorous diet as they are dominated by polysaccharide-fermenting taxa like *Lachnospiracea*, *Ruminococcocaceae* (Phylum *Firmicutes*) and *Prevotellaceae* (Phylum *Bacteroidetes*) (Amato et al., 2019; Greene et al., 2018, 2019b). Yet, while animals' foraging strategies may determine their basic gut microbial composition and diversity (Greene et al., 2018, 2019b), it appears that minor shifts in dietary patterns do not inflict detectable changes and are therefore unlikely drivers of between-group variation in gut microbiomes in this species.

Seasonal effects on microbial communities differ between years

Verreaux's sifakas' phylogenetic diversity was weakly linked to seasonality and most core phyla showed seasonal variation in relative abundances, reflecting dietary shifts of fruit and leave consumptions during the dry season. Our results are mainly in line with those of a prior study in the same population. Springer et al. (2017) reported clear seasonal variation of *Firmicutes-Bacteroidetes* ratios, whereas we did not

detect any seasonal changes in *Bacteroidetes*. With progression of the dry season, general food availability decreases and sifakas increase their intake of other plant parts, like barks, stems and flowers, leading to an increased fibre intake (Koch et al., 2017; Norscia et al., 2006) and thus a higher abundance of fibre-digesting *Firmicutes* (Flint et al., 2012; Gomez et al., 2016; Martens et al., 2014). Decreases in fruit intake are expected to result in lower abundances of *Bacteroidetes* (Gomez et al., 2016). However, the increase in consumption of various other plant parts during the late dry season might maintain the abundance of *Bacteroidetes*, which can digest a very broad array of mostly, but not exclusively, soluble substrates (Greene et al., 2019a; Martens et al., 2014; Wu et al., 2011). We believe that the contrasting patterns found in the study of Springer et al. (2017) and the present one might reflect annual variation in food availability and diet. In fact, we found monthly differences in phyla abundances to vary between years and animals had lower gut microbial diversities in 2017 than in 2016.

The missing puzzle pieces

Notably, about 30% of amplicon sequences belonging to 50% of all ASVs could not be assigned to any taxonomy, confirming results of prior studies in lemurs (Amato et al., 2019; Greene et al., 2019b, 2019a; Perofsky et al., 2019, 2017; Springer et al., 2017). This high proportion of unknown sequences is especially prevalent in members of the Indriidae family. The little microbial characterisations of taxa from Madagascar together with indriids' folivorous diets and complex gastrointestinal tracts are likely causes for the lack of taxonomic assignments. Interestingly, some of the unassigned taxa were high in abundance in some groups, yet, nearly completely absent in others (Figures 5b). This pattern implies that unclassified ASVs contribute to the divergence between our study groups' microbial communities. However, until these taxa are characterized, we cannot further explore this effect.

Conclusions

With this study, we contribute to the understanding of the relative importance of 1) environmental, 2) intrinsic, and 3) social factors on shaping gut microbial communities in wild animals. Our findings indicate that 1) environmental factors likely define the general set-up of species- or population-specific gut microbiota, while minor differences in microhabitat features or diets among local groups do not seem to inflict detectable variation. 2) Kinship plays an important role for the development of individual microbial patterns, however, whether these effects derived from increased proximity and interactions between kin or from genetic inheritance remains to be studied. Importantly, kinship effects seem to depend on species-specific frequencies of social contact, as social transmission can potentially overwrite microbiota acquired via kin. 3) Life in permanent social groups can promote the convergence of gut microbial communities. However, variation in species' social systems affects microbial dispersal opportunities, which is why the degree to which social interactions affect individual gut microbiota may vary across

species. More comprehensive studies across species with varying social systems will therefore help to shed more light on the co-evolutionary dynamics that shaped host-microbiota relationships.

Acknowledgments

We are grateful to the Malagasy Ministère de l'Environnement, the Departement de Biologie Ecologie et Conservation Animale de l'Université d'Antananarivo and the Centre National de Formation, d'Etudes et de Recherche en Environnementet Foresterie de Morondava for supporting our research in Kirindy Forest. We also thank Mamy Razafindrasamba and Tiana Andrianjanahary for their help in data collection, Dr Roger Mundry for statistical advice, Virgile Manin and the other members of the DFG research unit "Sociality and Health in Primates" (FOR 2136) for their precious remarks and constructive discussions. This research was funded by the Deutsche Forschungsgemeinschaft (DFG), grant number Ka 1082/29-2, awarded to PMK.

Ethical approval

Statement of ethical approval, approval of research protocols and capture procedures were approved by a committee of the Ministry for the Environment, Water and Forests of Madagascar (MINEEF). All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This article does not contain any studies with human participants performed by any of the authors.

Author contributions

PMK, CF, and KR designed the study. KR performed data collection and conducted the lab work. KR and DS and analysed the data. KR drafted the manuscript and all authors contributed to writing and revising of the manuscript.

Appendix: Chapter 4

This supplementary file contains more detailed information on:

(1) Supplemental Methods

Home range overlap

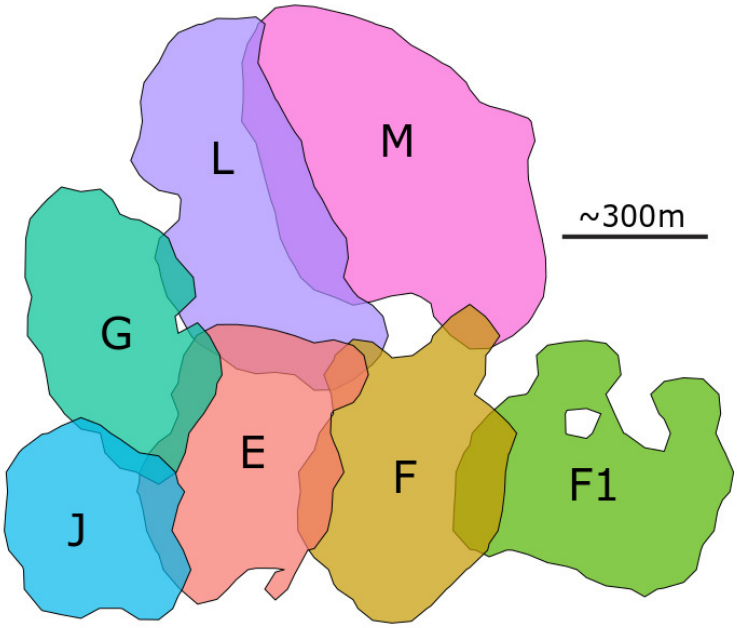


Figure S1 Illustration of home range locations and overlaps of all study groups. Areas indicate average 95% Kernels over the complete study period.

(2) Supplemental Results

Beta diversity (GUniFracs)

Within- and between-individual differences on microbiome compositions

Table S1 Comparing GUniFrac distances within and between group members in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 455, $N_{ID\ dyads}$ = 153).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	0.123	0.004	0.114	0.131	0.119	0.126	[c]	[c]	[c]
Same ID (yes)[d]	-0.019	0.003	-0.025	-0.011	-0.021	-0.017	26.366	1	**<0.001**
Season[e]							11.861[f]	3[f]	**0.008**[f]
late dry 2017	-0.006	0.002	-0.010	-0.002	-0.008	-0.005	[c]	[c]	[c]
early dry 2016	0.000	0.002	-0.003	0.004	-0.002	0.002	[c]	[c]	[c]
early dry 2017	-0.005	0.001	-0.008	-0.003	-0.006	-0.005	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. For intercepts, p-values would refer to estimated fGCM concentrations, when all covariates are at zero. For main effects of predictors which are involved in interaction terms, p-values refer only to the effect of that involved predictor with the interacting covariate at zero. This means the main effects of predictors involved in interactions depend on the value of the other main effects and are, therefore, not interpretable in themselves. Therefore, we consider P values of main effects to be meaningful only when the predictors are not involved in an interaction.
[d] Manually dummy-coded with the season "no" being the reference category
[e] Manually dummy-coded with the season "late dry 2016" being the reference category
[f] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

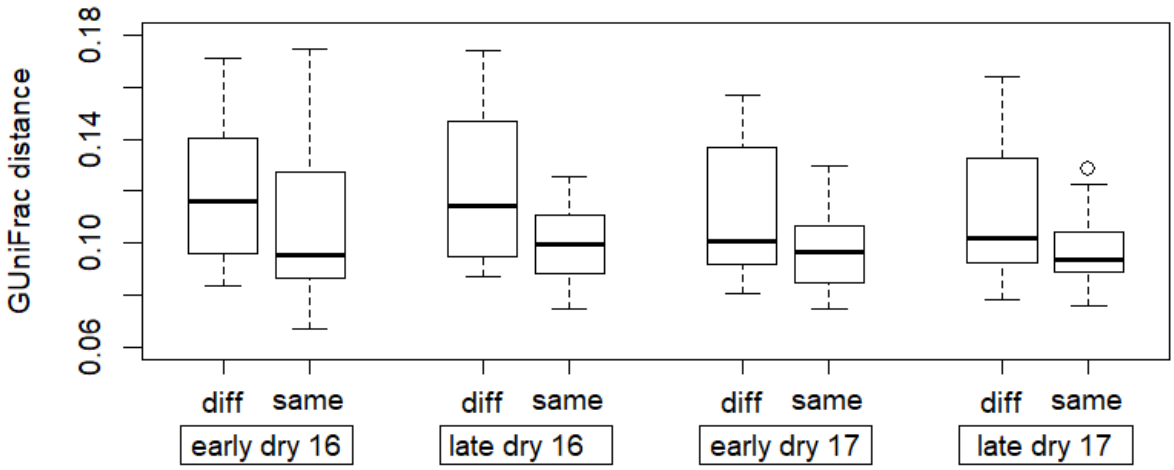


Figure S2 Comparison of microbiome dissimilarities between samples collected from the same individual and samples collected from different individuals living in the same group during four different field seasons. Lines indicate median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers.

Effects of body contact within groups (GUniFrac)

Table S2 Influence of body contact on GUniFrac distances (sqrt-transformed) among group member of seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 2856, $N_{ID\ dyads}$ = 86).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	0.378	0.003	0.372	0.384	0.376	0.380	[c]	[c]	[c]
Body contact[d]	0.001	0.001	-0.001	0.003	-0.001	0.001	0.223	1	0.637
Related (yes)[e]	-0.062	0.003	-0.069	-0.056	-0.065	-0.055	132.560	1	**<0.001**
Season[f]							14.317[g]	2[g]	**<0.001[g]**
late dry 2017	-0.011	0.003	-0.018	-0.003	-0.014	-0.007	[c]	[c]	[c]
early dry 2017	-0.008	0.002	-0.012	-0.005	-0.010	-0.007	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] z-transformed, mean and SD of the original values were 0.771 and 1.187 (min/h), respectively
[e] Manually dummy-coded with the season "no" being the reference category
[f] Manually dummy-coded with the season "late dry 2016" being the reference category
[g] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

Effects of maternal relatedness (GUniFrac)

Table S3 Influence of maternal relatedness on GUniFrac distances in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 1439, $N_{ID\ dyads}$ = 502).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	0.154	0.001	0.152	0.156	0.154	0.154	[c]	[c]	[c]
Related (yes)[d]	-0.030	0.006	-0.042	-0.018	-0.031	-0.029	[c]	[c]	[c]
Same group (yes)[e]	-0.011	0.003	-0.016	-0.005	-0.011	-0.010	[c]	[c]	[c]
Season[f]							257.245[g]	3[g]	**<0.001[g]**
late dry 2017	-0.008	0.001	-0.009	-0.006	-0.008	-0.008	[c]	[c]	[c]
early dry 2016	0.002	0.001	0.001	0.003	0.002	0.002	[c]	[c]	[c]
early dry 2017	-0.007	0.001	-0.008	-0.006	-0.007	-0.007	[c]	[c]	[c]
Related (yes) * Same group (yes)	-0.013	0.007	-0.027	0.000	-0.015	-0.012	3.679[h]	2[h]	0.055[h]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] Manually dummy-coded with the season "no" being the reference category
[e] Manually dummy-coded with the season "no" being the reference category
[f] Manually dummy-coded with the season "late dry 2016" being the reference category
[g] Values refer to the overall test of the effect of the predictor ("Season")
[h] Values refer to the overall test of the interaction "Related*Same Group", not the specific level indicated in the respective row

Effects of habitat overlap between groups (GUniFrac)

Table S4 Influence of habitat overlap on GUniFrac distances (ln-transformed) among seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 72, $N_{Group\ dyads}$ = 21).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-1.876	0.016	-1.910	-1.844	-1.883	-1.866	[c]	[c]	[c]
Overlap[d]	0.004	0.006	-0.009	0.016	0.001	0.010	0.286	1	0.593
Season[e]							42.066[f]	3[f]	**<0.001[f]**
late dry 2017	-0.057	0.007	-0.071	-0.043	-0.060	-0.054	[c]	[c]	[c]
early dry 2016	0.000	0.008	-0.017	0.017	-0.003	0.005	[c]	[c]	[c]
early dry 2017	-0.046	0.008	-0.062	-0.030	-0.049	-0.043	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] z-transformed, mean and SD of the original values were 0.045 and 0.063, respectively
[e] Manually dummy-coded with the season "late dry 2016" being the reference category
[f] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

Effects of diet dissimilarity between groups (GUniFrac)

Table S5 Influence of diet dissimilarity (Bray-Curtis) on GUniFrac distances (ln-transformed) among seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 57, $N_{Group\ dyads}$ = 21).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	-1.882	0.016	-1.913	-1.851	-1.888	-1.871	[c]	[c]	[c]
Diet dissimiliarity[d]	-0.004	0.006	-0.017	0.009	-0.007	-0.001	0.399	1	0.528
Season[e]							34.162[f]	2[f]	**<0.001[f]**
late dry 2017	-0.059	0.007	-0.072	-0.045	-0.062	-0.055	[c]	[c]	[c]
early dry 2017	-0.038	0.008	-0.054	-0.022	-0.044	-0.034	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] z-transformed, mean and SD of the original values were 0.592 and 0.132, respectively
[e] Manually dummy-coded with the season "late dry 2016" being the reference category
[f] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

Alpha diversity (Phylogenetic diversity)

Effects of group membership, season, study year and diet

Table S6 Influence of various factors on PDs (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 519, N_{ID} = 41, N_{Group} = 7).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		4.521	0.020	4.483	4.560	4.508	4.575	[c]	[c]	[c]
Group[e]	F	0.044	0.021	0.006	0.088	0.034	0.060	22.056[d]	6[d]	**0.001**[d]
	F1	0.000	0.027	-0.051	0.051	-0.040	0.028	[c]	[c]	[c]
	G	0.035	0.023	-0.011	0.083	-0.008	0.063	[c]	[c]	[c]
	J	-0.062	0.022	-0.103	-0.016	-0.108	-0.046	[c]	[c]	[c]
	L	0.035	0.026	-0.015	0.086	-0.011	0.051	[c]	[c]	[c]
	M	-0.118	0.027	-0.174	-0.064	-0.155	-0.099	[c]	[c]	[c]
Season (early)[e]		0.041	0.019	0.005	0.078	0.025	0.053	3.170	1	**0.075**
Year (2017)[f]		-0.118	0.012	-0.142	-0.097	-0.132	-0.108	85.651	1	**<0.001**
Sex (males)[g]		0.018	0.013	-0.007	0.042	0.010	0.024	1.840	1	0.175
Fruit intake[h]		-0.004	0.012	-0.029	0.022	-0.012	0.005	0.109	1	0.741
Leave intake[i]		0.015	0.011	-0.007	0.036	0.008	0.022	1.415	1	0.234

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictor ("Group") not the specific level indicated in the respective row
[e] Manually dummy-coded with group "E" and season "late dry" being the reference categories
[f] Manually dummy-coded with the year "2016" being the reference category
[g] Manually dummy-coded with "females" being the reference category
[h] z-transformed, mean and SD of the original values were 0.141and 0.175, respectively
[i] z-transformed, mean and SD of the original values were 0.516 and 0.214, respectively

Table S7 Results of post-hoc multiple comparisons of means using Tukey contrasts with adjusted p-values (Bonferroni) for comparisons of Phylogenetic diversities and Shannon indices among groups. Significant p-values are highlighted in bold.

Groups	PD		Shannon index*	
	Z	p adj	Z	p adj
F - E	2.148	0.667	-2.622	0.184
F1 - E	0.000	1.000	0.432	1.000
F1 - F	-1.821	1.000	2.548	0.227
G - E	1.485	1.000	0.691	1.000
G - F	-0.452	1.000	3.244	**0.025**
G - F1	1.278	1.000	0.152	1.000
J - E	-2.794	0.109	-1.371	1.000
J - F	-5.421	**<0.001**	1.215	1.000
J - F1	-2.365	0.379	-1.552	1.000
J - G	-4.232	**<0.001**	-2.026	0.898
L - E	1.376	1.000	1.084	1.000
L - F	-0.384	1.000	3.637	**0.006**
L - F1	1.217	1.000	0.491	1.000
L - G	0.023	1.000	0.392	1.000
L - J	3.871	**0.002**	2.397	0.347
M - E	-4.341	**<0.001**	-4.616	**<0.001**
M - F	-6.560	**<0.001**	-2.695	0.148
M - F1	-3.964	**0.002**	-4.316	**<0.001**
M - G	-5.611	**<0.001**	-5.114	**<0.001**
M - J	-2.135	0.689	-3.541	**0.008**
M - L	-5.179	**<0.001**	-5.335	**<0.001**

*Analyses and results for Shannon indices are described below.

Effects of group size (PD)

Table S8 Influence of group size on PDs (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 519, N_{ID} = 41, N_{Group} = 7).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	4.505	0.025	4.452	4.556	4.496	4.534	[c]	[c]	[c]
Group size[d]	0.015	0.028	-0.043	0.084	0.000	0.057	0.298	1	0.585
Year (2017)[e]	-0.126	0.014	-0.153	-0.096	-0.134	-0.116	17.393	1	**<0.001**
Sex (male)[e]	0.014	0.016	-0.018	0.045	0.004	0.022	0.776	1	0.378
Season (early dry)[e]	0.052	0.018	0.015	0.089	0.035	0.080	5.251	1	**0.022**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 6.387 and 2.082, respectively
[e] Manually dummy-coded with the year "2016", "females" and "late dry season" being the reference categories

Effects of body contact within groups (PD)

Table S9 Influence of body contact on PDs (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 427, N_{ID} = 41, N_{Group} = 7).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	4.513	0.025	4.467	4.562	4.502	4.534	[c]	[c]	[c]
Body contact[d]	-0.010	0.007	-0.025	0.005	-0.014	-0.006	1.702	1	0.192
Year (2017)[e]	-0.115	0.016	-0.149	-0.082	-0.125	-0.100	15.494	1	**<0.001**
Sex (male)[e]	0.010	0.017	-0.023	0.045	-0.001	0.017	0.327	1	0.568
Season (early dry)[e]	0.038	0.018	0.001	0.073	0.018	0.047	3.299	1	**0.069**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 3.856 and 2.881 in min/h, respectively
[e] Manually dummy-coded with the year "2016", "females" and "late dry season" being the reference categories

Monthly changes of core phyla abundances

Table S10 Kruskal-Wallis tests and Dunn's tests testing the difference in monthly abundance of 8 bacterial phyla in the gut microbiota of wild Verreaux's sifakas in 2016. Significant p-values (<.05) are printed in bold

2016	Kruskal-Wallis test			Dunn's tests *p-values*				Mean monthly relative abundance (%)
Phylum	χ^2	*df*	*P*		April	May	September	
Actinobacteria	15.597	3	**0.001**	April	-	-	-	1.93
				May	0.308	-	-	2.21
				September	**0.013**	1	-	2.44
				October	1	0.152	**0.004**	1.87
Bacteroidetes	0.553	3	0.907	April	-	-	-	22.76
				May	-	-	-	22.76
				September	-	-	-	22.90
				October	-	-	-	22.15
Cyanobacteria	5.240	3	0.155	April	-	-	-	2.72
				May	-	-	-	2.42
				September	-	-	-	2.92
				October	-	-	-	2.77
Fibrobacteres	24.397	3	**<0.001**	April	-	-	-	3.96
				May	**0.032**	-	-	2.83
				September	0.284	1	-	3.18
				October	0.802	**<0.001**	**0.002**	4.74
Firmicutes	19.659	3	**<0.001**	April	-	-	-	23.63
				May	**0.005**	-	-	27.06
				September	**<0.001**	1	-	27.62
				October	0.531	0.557	0.083	25.42
Proteobacteria	12.653	3	**<0.001**	April	-	-	-	3.28
				May	1	-	-	3.18
				September	0.710	0.404	-	2.76
				October	**0.030**	**0.010**	1	2.42
Synergistetes	9.247	3	**0.026**	April	-	-	-	0.71
				May	1	-	-	0.69
				September	1	1	-	0.73
				October	0.087	0.199	**0.023**	0.62
Verrucomicrobia	45.856	3	**<0.001**	April	-	-	-	4.27
				May	0.164	-	-	3.16
				September	1	**0.021**	-	4.54
				October	**<0.001**	**<0.001**	**0.001**	6.34

Table S11 Kruskal-Wallis tests and Dunn's tests testing the difference in monthly abundance of 8 bacterial phyla in the gut microbiota of wild Verreaux's sifakas in 2017. Significant p-values (<.05) are printed in bold

2017	Kruskal-Wallis test			Dunn's tests *p-values*				Mean monthly relative abundance (%)
Phylum	χ^2	*df*	*P*		April	May	September	
Actinobacteria	30.488	3	**<0.001**	April	-	-	-	2.32
				May	1	-	-	2.46
				September	**0.002**	**<0.001**	-	1.85
				October	**0.007**	**<0.001**	1	1.97
Bacteroidetes	3.366	3	0.339	April	-	-	-	24.77
				May	-	-	-	23.24
				September	-	-	-	25.14
				October	-	-	-	24.06
Cyanobacteria	6.133	3	0.105	April	-	-	-	2.92
				May	-	-	-	3.05
				September	-	-	-	3.18
				October	-	-	-	2.58
Fibrobacteres	39.410	3	**<0.001**	April	-	-	-	2.97
				May	0.199	-	-	2.32
				September	1	**0.007**	-	3.52
				October	**<0.001**	**<0.001**	**0.037**	4.72
Firmicutes	25.132	3	**<0.001**	April	-	-	-	24.59
				May	**<0.001**	-	-	28.49
				September	**0.001**	1	-	28.18
				October	**<0.001**	1	1	28.64
Proteobacteria	51.328	3	**<0.001**	April	-	-	-	3.14
				May	1	-	-	3.12
				September	**<0.001**	**<0.001**	-	2.18
				October	**<0.001**	**<0.001**	1	2.02
Synergistetes	19.500	3	**<0.001**	April	-	-	-	0.87
				May	0.235	-	-	0.79
				September	**0.027**	1	-	0.76
				October	**<0.001**	0.095	0.808	0.67
Verrucomicrobia	33.399	3	**<0.001**	April	-	-	-	3.16
				May	1	-	-	3.05
				September	**<0.001**	**<0.001**	-	4.39
				October	**0.004**	**0.001**	1	4.03

(3) Further Analyses

a. Beta diversity (Bray-Curtis dissimilarity)

Effects of group membership, seasonality and individuals

Samples from individuals living in the same group had lower dissimilarity scores than samples from individuals living in different groups (Table S12, Figure S3). Within groups, samples from the same individuals were more similar than samples between group members (GLMM: χ^2 = 23.609, df = 1, p < 0.001, $R^2_{m/c}$ = 0.12/0.91) (Table S13, Figure S4).

Within- and between-individual differences on microbiome compositions (Bray-Curtis)

Table S12 Results of Mantel tests comparing Bray-Curtis dissimilarities between seven groups of Verreaux's sifakas

Season	$n_{samples}$	$n_{individuals}$	$\bar{x}_{same\ group}$	$\bar{x}_{different\ group}$	*P*
early dry 2016	92	29	0.415	0.615	**<0.001**
late dry 2016	116	29	0.402	0.619	**<0.001**
early dry 2017	155	39	0.476	0.595	**<0.001**
late dry 2017	156	36	0.365	0.608	**<0.001**

Table S13 Comparing Bray-Curtis dissimilarities within and between group members in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 455, $N_{ID\ dyads}$ = 153).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	$\chi^{2\,b}$	*df*	*P*
(Intercept)	0.426	0.022	0.384	0.469	0.407	0.454	[c]	[c]	[c]
Same ID (yes)[d]	-0.106	0.021	-0.147	-0.064	-0.126	-0.091	23.609	1	**<0.001**
Season[e]							5.248[f]	3[f]	0.152[f]
late dry 2017	-0.018	0.008	-0.033	-0.002	-0.023	-0.011	[c]	[c]	[c]
early dry 2016	-0.009	0.008	-0.025	0.008	-0.014	-0.005	[c]	[c]	[c]
early dry 2017	-0.011	0.006	-0.023	0.001	-0.015	-0.006	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details
[d] Manually dummy-coded with the season "no" being the reference category
[e] Manually dummy-coded with the season "late dry 2016" being the reference category
[f] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

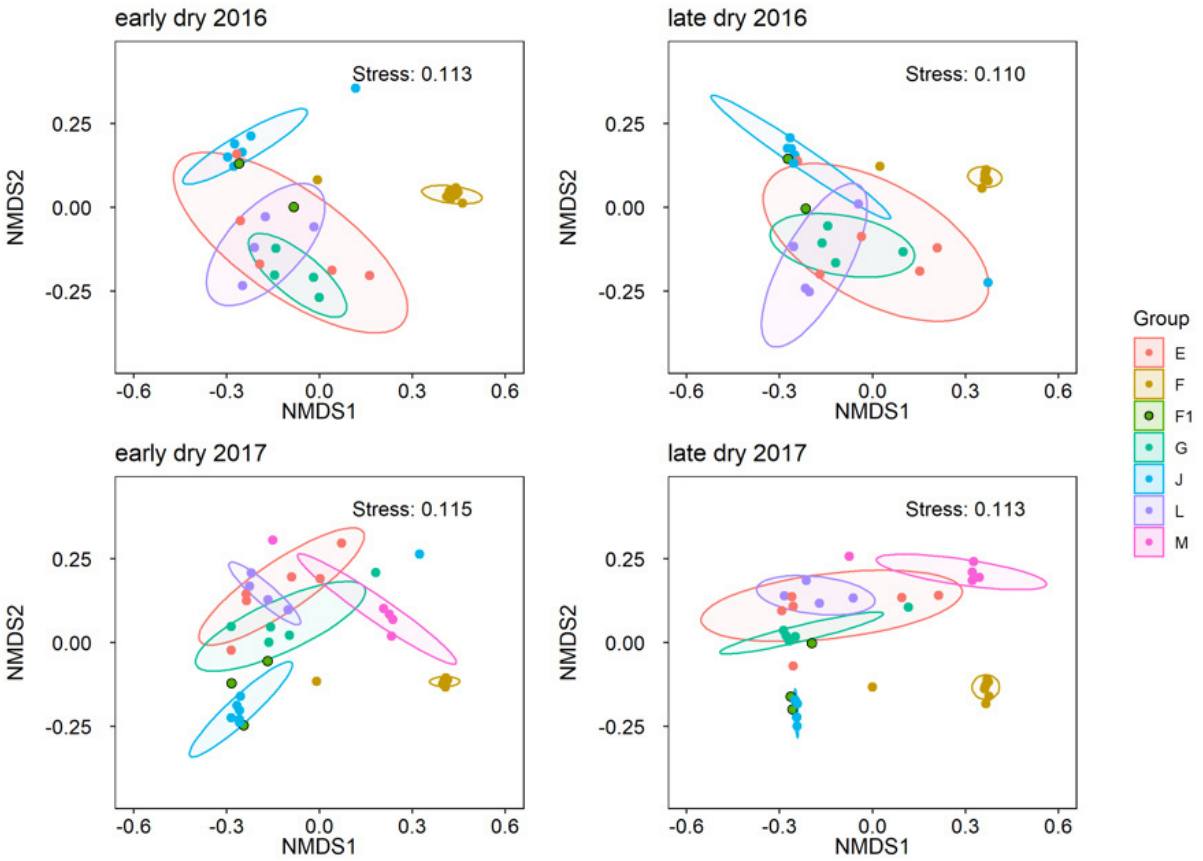


Figure S3 Nonmetric multidimensional scaling (NMDS) ordination of Verreaux's sifakas' gut bacterial composition data (Bray-Curtis) for each of the four field seasons. Data points represent individuals and colours indicate group membership. Ellipses indicate the 80% confidence ellipse for each group. For group F1, not enough data points were present to create ellipses, so we outlined the data points for better visibility. We collected several samples per individual per season, however, here we only plotted one data point per animal per season, based on average dyadic beta dissimilarity per field season, to facilitate the overview.

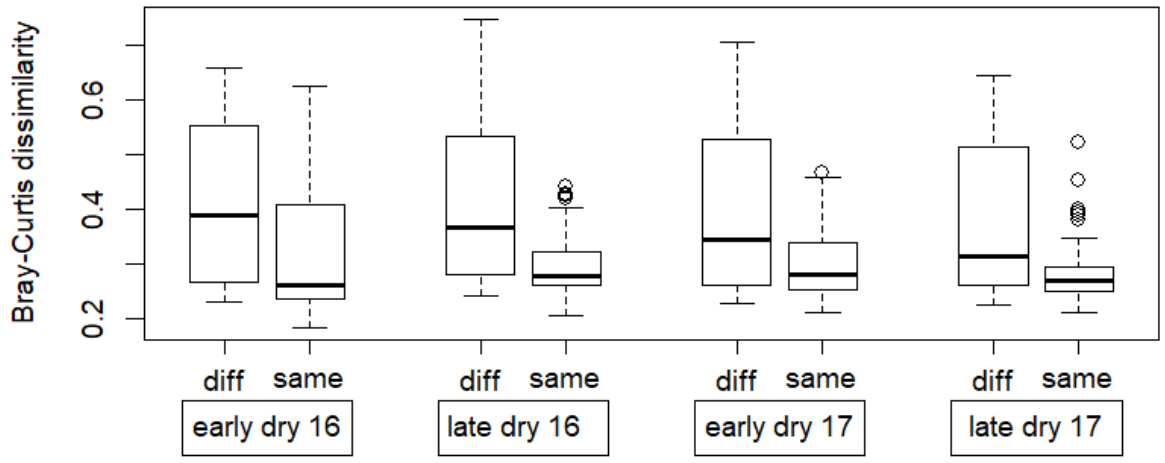


Figure S4 Comparison of Bray-Curtis dissimilarities between samples collected from the same individual and samples collected from different individuals living in the same group during for different field seasons. Boxplots comprise sample comparisons between all samples collected during the respective field seasons. Lines indicate median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers

Effects of body contact within groups (Bray-Curtis)

The model examining effects of the time group members spent in body contact on Bray-Curtis dissimilarities was not significant (χ^2 = 0.831, df = 1, p = 0.362, $R^2_{m/c}$ = 0.66/0.77) (Table S14).

Table S14 Influence of body contact on Bray-Curtis dissimilarities (sqrt-transformed) among group members of seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 2856, $N_{ID\ dyads}$ = 86).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^2 [b]	*df*	*P*
(Intercept)	-0.609	0.039	-0.685	-0.533	-0.650	-0.558	[c]	[c]	[c]
Body contact[d]	0.008	0.009	-0.009	0.026	-0.003	0.015	0.831	1	0.362
Related (yes)[e]	-0.635	0.025	-0.686	-0.586	-0.665	-0.522	174.878	1	**<0.001**
Season[f]							6.385[g]	2[g]	**0.041[g]**
late dry 2017	-0.051	0.017	-0.087	-0.016	-0.065	-0.036	[c]	[c]	[c]
early dry 2017	-0.034	0.017	-0.067	0.003	-0.062	-0.020	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] z-transformed, mean and SD of the original values were 0.771 and 1.187 (min/h), respectively
[e] Manually dummy-coded with the season "no" being the reference category
[f] Manually dummy-coded with the season "late dry 2016" being the reference category
[g] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

Effects of maternal relatedness (Bray-Curtis)

The interaction between maternal relatedness and group membership was not significant (Full-reduced model comparison: χ^2 = 1.056, df = 1, p = 0.304), so we excluded it from the model. The model examining the effects of maternal relatedness on Bray-Curtis dissimilarities between individuals was highly significant (χ^2 = 168.123, df = 1, p < 0.001, $R^2_{m/c}$ = 0.62/0.96) (Table S15), as Bray-Curtis dissimilarities were lower among maternal relatives.

Table S15 Influence of maternal relatedness on Bray-Curtis dissimilarities in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 1439, $N_{ID\ dyads}$ = 502).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^2 [b]	*df*	*P*
(Intercept)	0.625	0.004	0.616	0.633	-0.237	-0.230	[c]	[c]	[c]
Related (yes)[d]	-0.233	0.016	-0.264	-0.200	-0.103	-0.096	168.129	1	**<0.001**
Same group (yes)[e]	-0.100	0.015	-0.129	-0.072	-0.237	-0.230	45.040	1	**<0.001**
Season[f]							31.516[g]	3[g]	**<0.001[g]**
late dry 2017	-0.014	0.003	-0.020	-0.009	-0.015	-0.014	[c]	[c]	[c]
early dry 2016	-0.007	0.003	-0.012	-0.002	-0.007	-0.006	[c]	[c]	[c]
early dry 2017	-0.008	0.002	-0.013	-0.003	-0.009	-0.008	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] Manually dummy-coded with the season "no" being the reference category
[e] Manually dummy-coded with the season "no" being the reference category
[f] Manually dummy-coded with the season "late dry 2016" being the reference category
[g] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

Effects of habitat dissimilarity, overlap and diet dissimilarity between groups (Bray-Curtis)

Habitat and Bray-Curtis dissimilarities between groups were not correlated (Pearson: r = -0.091, $n_{Group\ dyads}$ = 21, p = 0.694). The models examining effects of habitat overlap and diet dissimilarities on groups' Bray-Curtis dissimilarities were not significant either (habitat overlap: χ^2 = 0.027, df = 1, p = 0.870, $R^2_{m/c}$ = 0.01/0.97; diet dissimilarity: χ^2 = 0.210, df = 1, p = 0.647, $R^2_{m/c}$ = 0.01/0.97) (Tables S16 & S17).

Table S16 Influence of habitat overlap on Bray-Curtis dissimilarities (ln-transformed) among seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 72, $N_{Group\ dyads}$ = 21).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^2 [b]	*df*	*P*
(Intercept)	-0.506	0.020	-0.544	-0.467	-0.512	-0.494	[c]	[c]	[c]
Overlap[d]	0.001	0.008	-0.015	0.017	-0.005	0.009	0.027	1	0.870
Season[e]							7.863[f]	3[f]	**0.049**[f]
late dry 2017	-0.018	0.009	-0.036	-0.001	-0.021	-0.014	[c]	[c]	[c]
early dry 2016	-0.029	0.012	-0.053	-0.007	-0.036	-0.019	[c]	[c]	[c]
early dry 2017	-0.011	0.006	-0.023	0.002	-0.014	-0.008	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details
[d] z-transformed, mean and SD of the original values were 0.045 and 0.063, respectively
[e] Manually dummy-coded with the season "late dry 2016" being the reference category
[f] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

Table S17 Influence of diet dissimilarity (Bray-Curtis) on Bray-Curtis dissimilarities (ln-transformed) among seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 57, $N_{Group\ dyads}$ = 21).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^2 [b]	*df*	*P*
(Intercept)	-0.506	0.020	-0.543	-0.468	-0.513	-0.494	[c]	[c]	[c]
Diet dissimiliarity[d]	0.002	0.004	-0.006	0.010	0.000	0.003	0.210	1	0.647
Season[e]							4.676[f]	2[f]	**0.097**[f]
late dry 2017	-0.017	0.009	-0.035	0.000	-0.021	-0.013	[c]	[c]	[c]
early dry 2017	-0.011	0.006	-0.024	0.001	-0.016	-0.008	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] z-transformed, mean and SD of the original values were 0.592 and 0.132, respectively
[e] Manually dummy-coded with the season "late dry 2016" being the reference category
[f] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

b. Alpha diversity (Shannon index)

Effects of group membership, season, study year and diet

The model examining effects of group membership, season (early dry vs. late dry), study year and diet on individual Shannon indices was significant (χ^2 = 46.152, df = 9, p < 0.001, $R^2_{m/c}$ = 0.35/0.51) (Table S18). In detail, group membership and study year affected individual alpha diversity. Members of group M had lower Shannon indices than all groups except for group F. Group F had lower Shannon indices than groups E, G, J and L (Figure S5 a). In 2017, all animals had lower Shannon indices than in 2016 (Figure S5 b). No correlations were found for seasons and fruit and leave intake rates (Figure S5 c, d & e).

Effects of group size (Shannon)

The second model, examining effects of group size on Shannon indices was not significant (χ^2 = 3.407, df = 1, p = 0.065, $R^2_{m/c}$ = 0.16/0.52) (Table S19) (Figure S5 f).

Effects of body contact within groups (Shannon)

The model examining effects of time spent in body contact within groups was not significant (χ^2 = 0.108, df = 1, p = 0.742, $R^2_{m/c}$ = 0.11/0.54) (Table S20, Figure S5 g).

Table S18 Influence of various factors on Shannon indeces (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 519, N_{ID} = 41, N_{Group} = 7).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^2 [b]	*df*	*P*
(Intercept)		1.637	0.012	1.612	1.660	1.601	1.641	[c]	[c]	[c]
Group[e]	F	-0.033	0.013	-0.058	-0.007	-0.041	-0.028	20.295[d]	6[d]	**0.002**[d]
	F1	0.007	0.017	-0.025	0.041	-0.006	0.040	[c]	[c]	[c]
	G	0.010	0.015	-0.018	0.04	0.004	0.044	[c]	[c]	[c]
	J	-0.019	0.014	-0.045	0.009	-0.025	0.015	[c]	[c]	[c]
	L	0.016	0.015	-0.014	0.048	0.010	0.050	[c]	[c]	[c]
	M	-0.071	0.015	-0.101	-0.042	-0.085	-0.038	[c]	[c]	[c]
Season (early dry)[e]		-0.008	0.006	-0.020	0.005	-0.011	-0.004	1.276	1	0.259
Year (2017)[f]		-0.036	0.004	-0.044	-0.029	-0.038	-0.034	17.664	1	**<0.001**
Sex (males)[g]		-0.008	0.008	-0.025	0.007	-0.014	-0.003	1.039	1	0.308
Fruit intake[h]		-0.005	0.003	-0.011	0.002	-0.008	-0.002	1.564	1	0.211
Leave intake[i]		0.000	0.003	-0.006	0.006	-0.001	0.001	0.000	1	0.992

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictor ("Group"), not the specific level indicated in the respective row
[e] Manually dummy-coded with group "E" and season "late dry" being the reference categories
[f] Manually dummy-coded with the year "2016" being the reference category
[g] Manually dummy-coded with "females" being the reference category
[h] z-transformed, mean and SD of the original values were 0.141and 0.175, respectively
[i] z-transformed, mean and SD of the original values were 0.516 and 0.214, respectively

Table S19 Influence of group size on Shannon indices (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 519, N_{ID} = 41, N_{Group} = 7).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	1.622	0.011	1.600	1.645	1.616	1.634	[c]	[c]	[c]
Group size[d]	-0.012	0.006	-0.026	0.001	-0.019	-0.008	3.407	1	0.065
Year (2017)[e]	-0.033	0.004	-0.041	-0.026	-0.035	-0.030	14.554	1	**<0.001**
Sex (male)[e]	-0.006	0.009	-0.023	0.013	-0.012	-0.001	0.386	1	0.534
Season (early dry)[e]	-0.017	0.004	-0.026	-0.008	-0.022	-0.016	10.628	1	**0.001**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 6.387 and 2.082, respectively
[e] Manually dummy-coded with the year "2016", "females" and "late dry season" being the reference categories

Table S20 Influence of body contact on Shannon indices (ln-transformed) in seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 427, N_{ID} = 41, N_{Group} = 7).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)	1.617	0.012	1.600	1.645	1.610	1.629	[c]	[c]	[c]
Body contact[d]	0.001	0.002	-0.026	0.001	0.000	0.002	0.108	1	0.742
Year (2017)[e]	-0.025	0.005	-0.041	-0.026	-0.029	-0.021	7.886	1	**0.005**
Sex (male)[e]	-0.006	0.010	-0.023	0.013	-0.013	-0.001	0.397	1	0.529
Season (early dry)[e]	-0.021	0.005	-0.026	-0.008	-0.024	-0.018	11.167	1	**0.001**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 3.856 and 2.881 in min/h, respectively
[e] Manually dummy-coded with the year "2016", "females" and "late dry season" being the reference categories

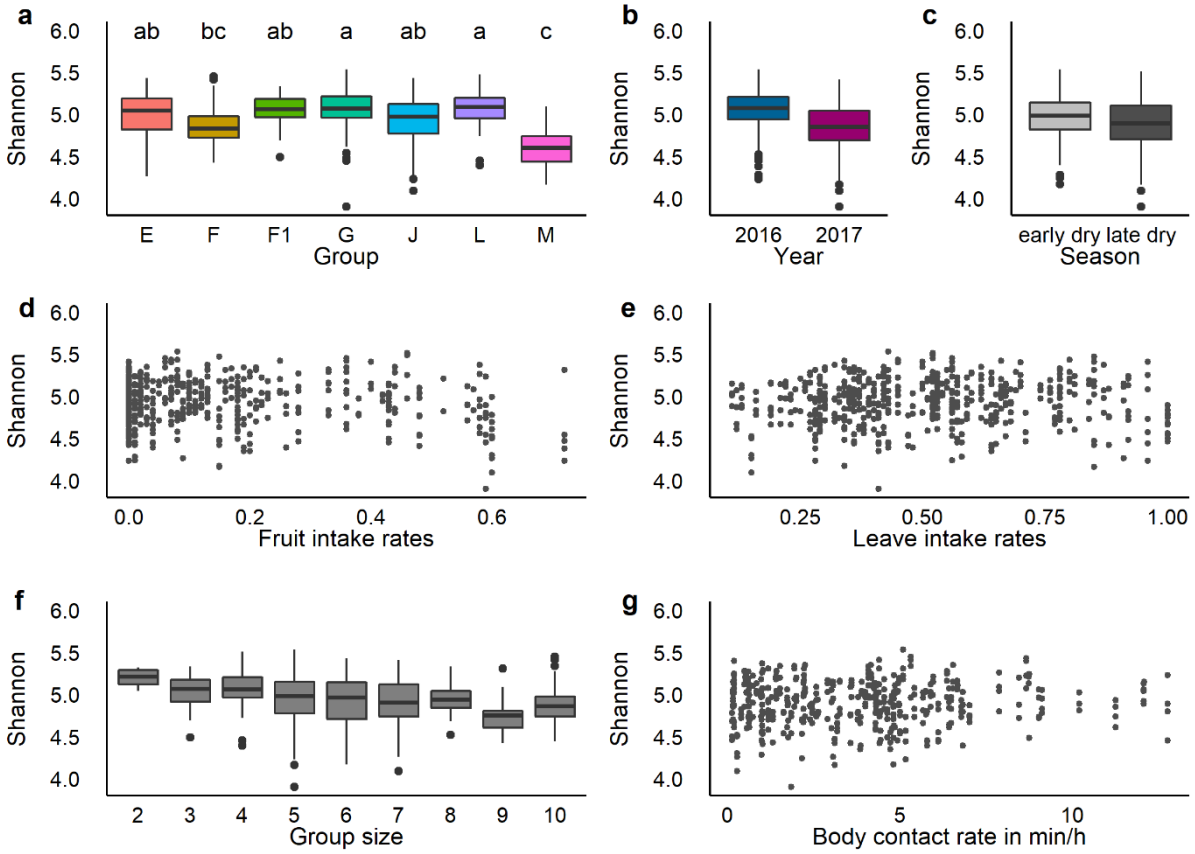


Figure S5 Influence of various factors on alpha diversity (Shannon index). Coloured graphs indicate significant effects. a, b & c) Influence of group identity, study year and season. Boxplots comprise all individual samples with lines indicating median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers. d & e) Influence of mean fruit and leave intake rates per field season. f) Influence of mean group size per field season. g) Influence of mean time spent in body contact per field season

c. Comparisons with Perofsky et al. (2017): Social network statistics and microbiomes

Like Perofsky et al. (2017), we constructed social networks based on grooming interactions for each of three field seasons from the data set described in the main paper. We calculated grooming indices as the time two individuals spent grooming divided by the combined focal observation times of both individual. Grooming indices were used as weights for network edges. We described the social connectivity within groups via edge densities, i.e. the number of edges divided by the number of possible edges. Moreover, we calculated inverse weighted path lengths (i.e. the smallest weight of inverse weights of edges) as a measure for social distance between each group member dyad and we computed weighted degree centrality for each individual (i.e. the sum of each individual's edge weights) from the grooming network. Social networks and network statistics were constructed with the package *igraph* (version 1.2.4.1) (Csárdi and Nepusz, 2006).

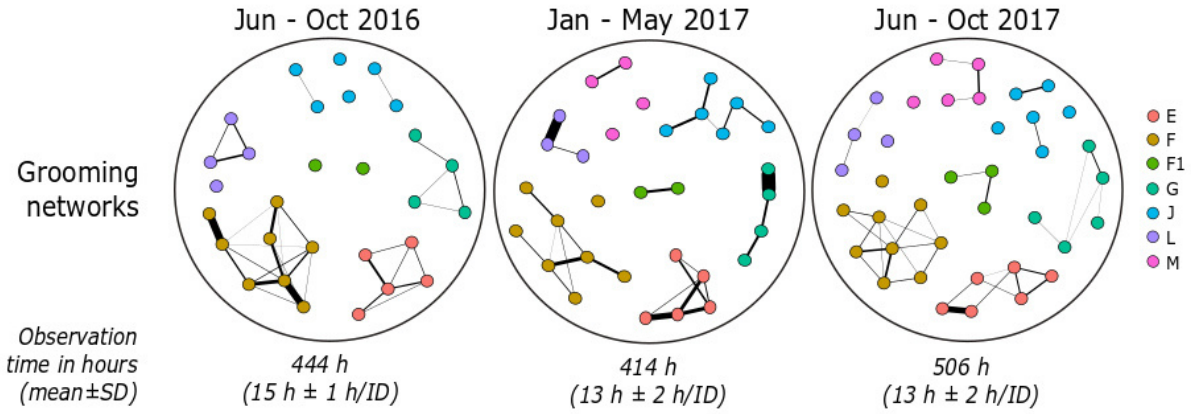


Figure S6 Social networks based on grooming interactions observed in the 3 months prior to and during field seasons of microbiome sampling among seven sifaka groups. Nodes represent individuals and lines represent grooming interactions between individuals with thicker lines reflecting higher grooming indices.

Based on the grooming networks, we conducted three analyses in similar manner as Perofsky et al. (2017): 1) To examine whether individuals in groups with higher average edge densities, i.e. social connectedness, share more similar microbiomes, we used Pearson correlations of average edge densities per group per field season with average dyadic beta diversities between group members. 2) We examined the effects of "social distance" (measured as inverse weighted path lengths) on GUniFrac distances between group members by applying GLMMs. Individual dyads and group ID were used as random effects and field seasons as random slopes. To control for effects of field season and maternal relatedness (see below), we included both factors as fixed effects. 3) To assess whether group members with stronger ties (measured as weighted degree centrality) have higher PDs, we applied another GLMM. We included study year and sex as fixed effects, group and animal ID as random effects and study year as random slope. Additionally, we included weighted degree centrality as random slope per ID.

Results and discussion of social network statistics

1) Pearson correlations examining links between groups' edge densities and individuals' GUniFrac distances and Bray-Curtis dissimilarities yielded in varying results across the field seasons. There was no correlation during the late dry season 2016 (GUniFrac: r= 0.054, p = 0.665; Bray-Curtis: r= 0.007, p = 0.957), while during the early and late dry season 2017 we found groups with greater social connectedness to have less homogenous microbiomes (early dry 2017: GUniFrac: r = 0.377, p < 0.001; Bray-Curtis: r= 0.303, p = 0.002; late dry 2017: GUniFrac: r = 0.288, p = 0.007; Bray-Curtis: r= 0.345, p = 0.001) (Figure S7).

2) The models examining the effects of social distance on GUniFrac distances between group members was significant (χ^2 = 4.765, df = 1, p = 0.029, $R^2_{m/c}$ = 0.54/0.62), while the model on Bray-Curtis dissimilarities was not (χ^2 = 1.825, df = 1, p = 0.177, $R^2_{m/c}$ = 0.66/0.79). Thus, dyads with stronger grooming relationships shared less closely related bacteria, however, this effect was fairly weak (Table S21).

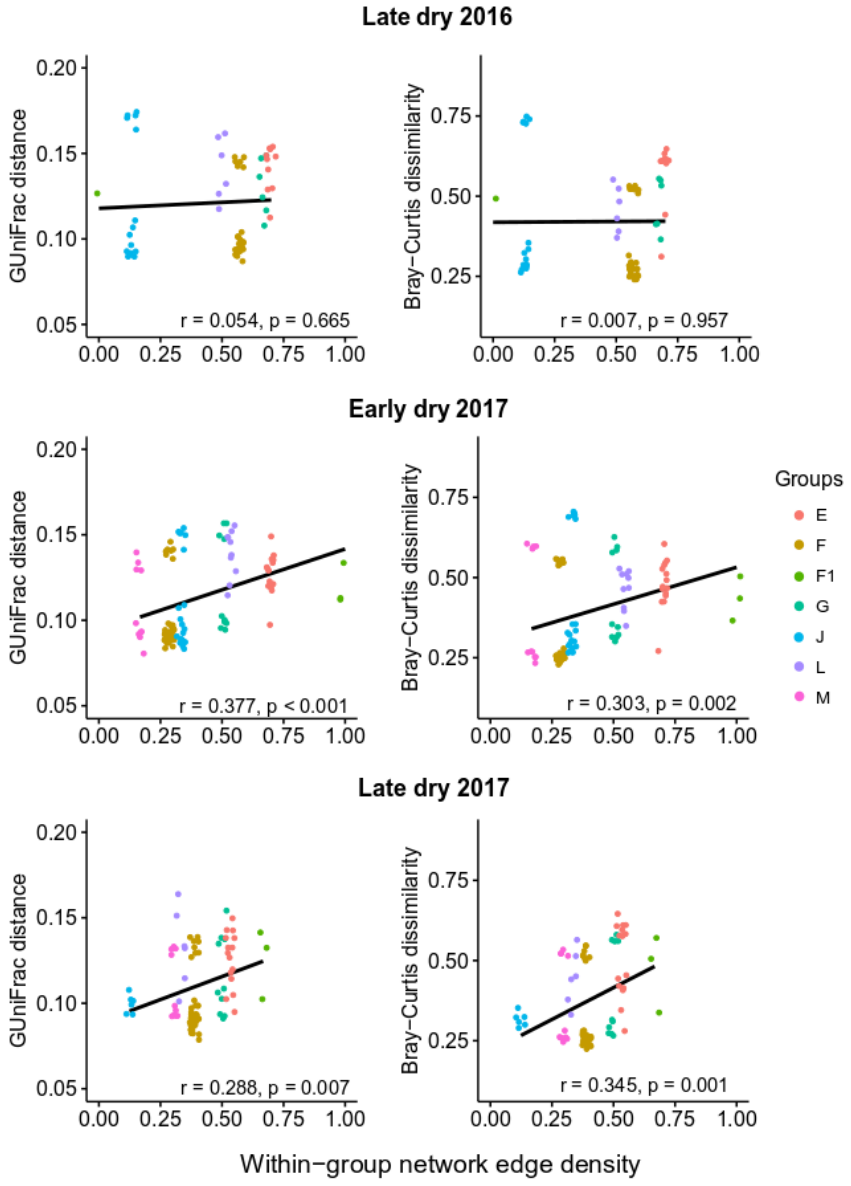


Figure S7 Effects of groups' average edge densities on microbiome dissimilarities among group members. Data points represent mean beta diversity between group members per field seasons. Lines indicate regression lines of Pearson correlations.

Table S21 Influence of social distance (measured as weighted path lengths) on GUniFrac distances (ln-transformed) and Bray-Curtis dissimilarities (sqrt-transformed) among group members of seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 2252, $N_{ID\ dyads}$ = 76, N_{Grous} = 6).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
GUniFrac Model									
(Intercept)	0.377	0.003	0.370	0.384	0.374	0.381	[c]	[c]	[c]
Social distance[d]	0.003	0.001	0.000	0.006	0.001	0.005	4.765	1	**0.029**
Related (yes)[e]	-0.062	0.003	-0.068	-0.057	-0.067	-0.052	126.925	1	**<0.001**
Season[f]							5.603[g]	2[g]	0.061[g]
late dry 2017	-0.009	0.006	-0.022	0.003	-0.015	0.000	[c]	[c]	[c]
early dry 2017	-0.008	0.002	-0.013	-0.004	-0.010	-0.005	[c]	[c]	[c]
Bray-Curtis Model									
(Intercept)	-0.601	0.053	-0.702	-0.492	-0.647	-0.539	[c]	[c]	[c]
Social distance[d]	0.015	0.011	-0.007	0.038	0.000	0.044	1.825	1	0.177
Related (yes)[e]	-0.649	0.022	-0.693	-0.608	-0.675	-0.530	166.756	1	**<0.001**
Season[f]							2.956[g]	2[g]	0.228[g]
late dry 2017	-0.044	0.048	-0.135	0.049	-0.077	-0.007	[c]	[c]	[c]
early dry 2017	-0.038	0.019	-0.083	0.000	-0.052	-0.021	[c]	[c]	[c]

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table A.1 for details.
[d] z-transformed, mean and SD of the original values were 29.951 and 32.371, respectively
[e] Manually dummy-coded with the season "no" being the reference category
[f] Manually dummy-coded with the season "late dry 2016" being the reference category
[g] Values refer to the overall test of the effect of the predictor ("Season"), not the specific level indicated in the respective row

3) Individuals with stronger ties within their groups (measured as weighted degree centrality) did not have greater PDs (χ^2 = 0.710, df = 1, p = 0.399, $R^2_{m/c}$ = 0.12/0.26) or Shannon indices (χ^2 = 0.125, df = 1, p = 0.723, $R^2_{m/c}$ = 0.11/0.56) (Table S22).

Table S22 Influence of individual weighted degree centrality on GUniFrac distances (ln-transformed) and Bray-Curtis dissimilarities (sqrt-transformed) among group members of seven groups of Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 396, N_{Groups} = 7, N_{ID} = 41).

Term	Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
				PD Model					
(Intercept)	4.523	0.023	4.480	4.567	4.512	4.579	[c]	[c]	[c]
WDC[d]	0.008	0.010	-0.012	0.029	0.001	0.021	0.710	1	0.399
Year(2017)[e]	-0.117	0.016	-0.147	-0.084	-0.165	-0.107	16.361	1	**<0.001**
Sex (m)[e]	0.002	0.016	-0.03	0.031	-0.007	0.007	0.012	1	0.914
Season (early dry)[e]	0.033	0.018	-0.002	0.067	0.007	0.043	3.007	1	0.083
				Shannon Model					
(Intercept)	1.618	0.013	1.593	1.644	1.610	1.629	[c]	[c]	[c]
WDC[d]	-0.001	0.003	-0.008	0.006	-0.003	0.001	0.125	1	0.723
Year(2017)[e]	-0.023	0.006	-0.035	-0.012	-0.028	-0.020	7.150	1	**0.007**
Sex (m)[e]	-0.008	0.010	-0.027	0.013	-0.015	-0.002	0.564	1	0.452
Season (early dry)[e]	-0.024	0.006	-0.036	-0.012	-0.027	-0.022	9.432	1	**0.002**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] z-transformed, mean and SD of the original values were 6.387 and 2.082, respectively
[e] Manually dummy-coded with the year "2016", "females" and "late dry season" being the reference categories

Altogether, grooming network analyses in our study population yielded contrasting patterns compared to a study in a differen population (Perofsky et al., 2017). Based on weighted grooming networks, we found individuals in groups with higher connectedness and group members that groom each other more to share less similar microbiomes. Moreover, no correlation was found between individual network centrality and microbial diversity. While no associations between affiliative behaviors and microbial diversity have been reported before and are also congruent with our other results (see above), the findings that groups and dyads which engage more in grooming share less similar microbiomes seem counterintuitive. We doubt that our data captured all relevant grooming connections within groups, despite our large data set containing hundreds of hours of behavioural observations. Grooming behaviour in sifakas is relatively rare and short (Lewis, 2010) and dense observation schedules are required to collect sufficient data to enable the construction of reliable grooming networks. Yet, such sampling effort is difficult to implement in wild populations. Weighted grooming networks, which are based on only a few minutes of dyadic interactions observed over months, are prone to contain incomplete information about animals' social connectivity. We therefore believe that grooming network statistics – if they are not based on intense observation schedules - cannot provide meaningful answers to questions addressing the impact of social interactions on horizontal bacterial transmissions in Verreaux's sifakas.

d. Leave and fruit intake per group per season

We applied two binomial models with beta error distribution structures and a logit link function using the *glmmTMB* package (version 0.2.3) (Brooks et al., 2017) to examine variation in leave and fruit consumption between group. We used mean intake rates on leaves or fruits per individual per season as response variables, group ID and season (early dry or late dry) as predictors variables and group and animal ID as random effect. P-values for individual effects were based on likelihood ratio tests comparing the full with the respective null models using the *drop1* function (Barr et al., 2013). We encountered no issues when checking for model stability and overdispersion and assessed confidence intervals with the *confint* function of the *glmmTMB* package.

Both models were significant (Leaves: χ^2 = 24.702, df =7, p > 0.001; Fruits: χ^2 = 32.118, df =7, p > 0.001) (Tables S23 and S24). Intake rates of both, leaves and fruits, were higher during the early dry season, when more food was available (Kappeler and Fichtel, 2012; Rudolph et al., 2019), indicating that sifakas increase their intake of other food items, e.g. flowers, barks or seeds (Koch et al., 2017) during the late dry season. Groups did not differ significantly in their leave and fruit consumption (Figure S8).

Table S23 Variation in leave consumption between groups and seasons in Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 133, N_{Groups} = 7, N_{ID} = 41).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		-0.032	0.211	-0.446	0.383	-0.260	0.042	[c]	[c]	[c]
Group[e]	F	-0.125	0.251	-0.617	0.368	-0.225	0.007	3.857[d]	6[d]	0.696[d]
	F1	-0.273	0.343	-0.946	0.400	-0.374	-0.141	[c]	[c]	[c]
	G	-0.325	0.292	-0.897	0.246	-0.426	-0.195	[c]	[c]	[c]
	J	-0.015	0.279	-0.562	0.531	-0.254	0.133	[c]	[c]	[c]
	L	-0.478	0.298	-1.062	0.105	-0.283	0.045	[c]	[c]	[c]
	M	-0.086	0.340	-0.753	0.580	-0.225	0.007	[c]	[c]	[c]
Season (early dry)[e]		0.721	0.153	0.422	1.020	0.599	0.930	20.688[d]	1[d]	**>0.001[d]**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictors ("Group", "Season"), not the specific level indicated in the respective row
[e] Manually dummy-coded with group "E" and season "late dry" being the reference categories

Table S24 Variation in fruit consumption between groups and seasons in Verreaux's sifakas; results of the full model (GLMM; $N_{Observations}$ = 133, N_{Groups} = 7, N_{ID} = 41).

Term		Est	SE	Lower CI	Upper CI	Min[a]	Max[a]	χ^{2} [b]	*df*	*P*
(Intercept)		-2.114	0.236	-2.577	-1.650	-2.605	-2.027	[c]	[c]	[c]
Group[e]	F	-0.516	0.272	-1.051	0.018	-0.640	-0.377	10.431[d]	6[d]	0.108[d]
	F1	-0.059	0.370	-0.783	0.666	-0.169	0.453	[c]	[c]	[c]
	G	0.163	0.301	-0.428	0.754	0.062	0.670	[c]	[c]	[c]
	J	-0.185	0.287	-0.748	0.378	-0.338	0.324	[c]	[c]	[c]
	L	0.445	0.316	-0.175	1.064	0.326	0.963	[c]	[c]	[c]
	M	-0.305	0.385	-1.060	0.450	-0.461	0.217	[c]	[c]	[c]
Season (early dry)[e]		0.902	0.178	0.552	1.251	0.750	1.150	24.231[d]	1[d]	**>0.001[d]**

[a] Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time
[b] Results of a likelihood ratio test comparing the full model with a reduced model lacking the respective term
[c] Not shown as not having a meaningful interpretation. See footnotes of Table S1 for details.
[d] Values refer to the overall test of the effect of the predictors ("Group", "Season"), not the specific level indicated in the respective row
[e] Manually dummy-coded with group "E" and season "early dry" being the reference categories

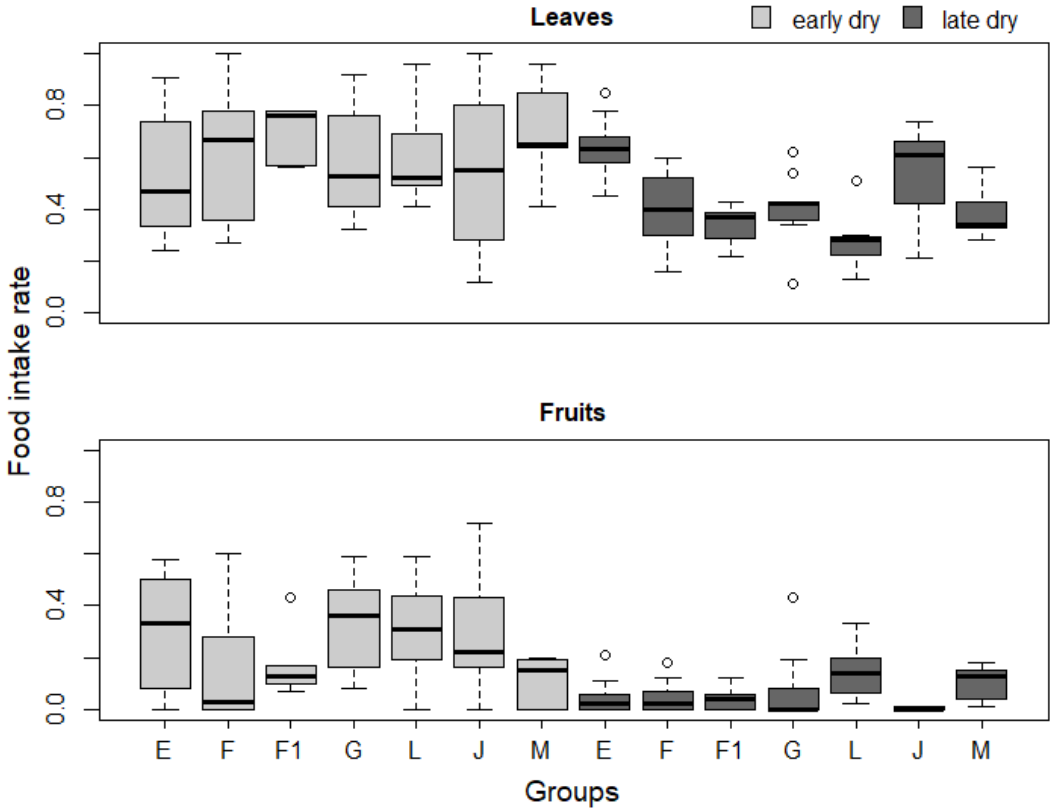


Figure S8 Average leave and fruit intake rates of Verreaux's sifaka groups during the early and late dry season. Boxplots comprise mean individual consumption rates per season with lines indicating median, upper and lower quartiles. Whiskers indicate +/- 1.5 interquartile ranges and small circles beyond whiskers indicate outliers

Chapter 5

General Discussion

5.1 A Brief Summary

Evidence from various scientific disciplines is accumulating that social behaviours crucially impact human and animal health. However, little is known about the proximate mechanisms underlying the sociality-health link. One reason for this limited understanding is the low number of longitudinal studies that systematically examined this relationship in wild populations (Kappeler et al., 2015; Silk, 2014). Here, I add needed data to this field of research by studying links between sociality and indicators of health in wild Verreaux's sifakas for two consecutive years. I examined various aspects of Verreaux's sifakas' group life, i.e. group size, group membership, rank, affiliative and agonistic interactions, and their potential associations with parasite infections, energy budgets and microbial communities. In the following, I will summarise the main findings of my thesis.

Study I – Group size, Health and Ecology

In the first study, I tested predictions of the *ecological constraints* and *the optimal group size hypothesis*, which link group size to condition and health. Group size had neither impact on groups' ranging patterns and daily activities nor on individual glucocorticoid metabolite concentrations or parasite richness, while seasonal variation in food availability and temperature differences affected the majority of variables. The study does not support the tested hypotheses and I conclude that there is no optimal group size in Verreaux's sifakas, presumably because group sizes of this species remain below the upper, ecologically "optimal" limits. It appears, that most folivorous mammals, like Verreaux's sifakas, are constrained in group size by social rather than ecological factors.

Study II – Dynamics and Determinants of Individual fGCM Concentrations

In the second study, I examined the potential impact of social and ecological factors on concentrations of fGCMs. Measures of fGCMs were correlated to seasonal variation in temperature, fruit availability and intake. Moreover, they were elevated during premating periods in males and gestation in females, while there was no link with agonistic or affiliative interactions, adult sex ratios, vigilance or scratch rates. Effects of male rank on fGCMs vary across years, indicating that energetic constraints on male rank may depend on extrinsic factors like annual variation of their social and ecological environments. I show that measures of glucocorticoids constitute valuable tools for studying energetic burdens of ecological and reproductive challenges in wild populations, while they seem to be insufficient indicators for immediate consequences of social and non-social behaviours that are not directly linked to energy budgets.

Study III – Exploring Between-Group Variation in Gut Microbial Communities

In the third study, I investigated the causes for between-group variation on gut microbial communities by correlating measures of gut microbial composition and diversity with data on social interactions, maternal relatedness, diet, habitat structure, habitat overlap and seasonality. Group membership and maternal relatedness, but not social interactions, affected dyadic gut microbial similarity, whereas none of the environmental predictors, i.e. habitat overlap, habitat dissimilarity and diet, explained variation in gut microbiomes between groups. Environmental factors seem to determine the general set-up of gut microbial compositions on a species- or population level, but finer-scaled environmental differences between local groups do not have detectable effects on gut communities. Kinship plays a large role for between-group variation in microbial communities however, other factors must also contribute to this effect since unrelated individuals had more similar microbiota with group members than relatives living in different groups. Rare physical contact between members of different groups and frequent physical contact among members of the same group may contribute to the here found group membership effects, however, more research is required to confirm this assumption.

In summary, most of the here found behavioural and physiological differences between groups or individuals were not affected by social variables but could be explained by seasonal changes in animals' physical environments. In light of the two main costs of sociality, i.e. a) social transmission of pathogens and microbes, and b) increased susceptibility to diseases owing to social stress (Kappeler et al., 2015), I found some evidence for the former but no indication for the latter. Concerning a), I could show that group living had a clear impact on individuals' gut microbiota, which may have important implications for their health, however, state-of-the-art knowledge on host-microbiota interactions remains too poor to derive reliable conclusions about health-effects. As for b), I found no association between social interactions and competition within or between groups with individual fGCM concentrations and parasite infections. The results of my thesis, therefore, indicate that health-related consequences of different aspects of group living in Verreaux's sifakas are limited to effects caused by social proximity but not social interactions with group members. A closer look at Verreaux's sifakas' behavioural ecology might explain some of these findings.

5.2 Limited Health-Related Consequences of Sociality in Verreaux's Sifakas

- A Consequence of the Mysterious "Lemur Syndrome"?

Primates show considerable diversity and flexibility in their social organisations, ranging from solitary- and pair-living up to the formation of multi-level societies (Silk and Kappeler, 2017). Socioecological theory has derived general frameworks which provide major contributions to understanding variation in anthropoid primates' social systems (Clutton-Brock and Harvey, 1977; Crook and Gartlan, 1966; Emlen

and Oring, 1977; Kappeler and van Schaik, 2002; Koenig et al., 2013). However, lemur societies have puzzled scientists for decades with the so-called "lemur syndrome" - an array of patterns that are not found in anthropoid primates and have proven difficult to be explained by socioecological models (Eberle and Kappeler, 2004; Kappeler and Fichtel, 2015; Kappeler and Schäffler, 2007). This phenomenon comprises behavioural, morphological and ecological traits, including even adult sex ratios (Kappeler et al., 2009b), female dominance (Jolly, 1984; van Schaik and Kappeler, 1996), and the lack of male-sexual dimorphism regardless of mating system (Kappeler and Schäffler, 2007). Previous attempts to understand the evolution of the lemur syndrome proposed adaptations to Madagascar's harsh and unpredictable environment (Dewar and Richard, 2007; Kappeler et al., 2019; Wright, 1999; but see Federman et al., 2017), relaxed male mating competition (Hrdy, 2009; Kappeler, 1993) or a combination of evolutionary and developmental processes based on chronic maternal stress (Kappeler and Fichtel, 2015) as possible explanations. Thus, lemurs express unique patterns in social and sexual behaviours, which might explain the relatively low health-related costs and benefits of their social life.

"Pacifism" Reduces Health-Related Costs of Sociality

Social interactions play a key role for individual health (Kappeler et al., 2015; Ostner and Schülke, 2018) as they can mediate physiological stress responses (Raulo and Dantzer, 2018), enhance risks of pathogen transmission (Poulin, 2018) and facilitate the exchange of microbial-mediated pathogen resistance (Ezenwa et al., 2016). Affiliative and agonistic interactions are part of daily life in social groups and enable animals to establish and maintain social relationships, to determine dominance positions and to gain access to mating opportunities. However, compared to most anthropoid primates, lemurs devote little time to social interactions (Erhart and Overdorff, 2008; Rasolonjatovo and Irwin, 2019; Wheeler et al., 2013), presumably affecting the health-consequences of their social life.

Agonistic interactions are especially important for establishing social hierarchies (Drews, 1993; Wheeler et al., 2013). In Verreaux's sifakas, hierarchies are linear with adult females at the highest positions (Kappeler and Schäffler, 2007; Kraus et al., 1999). Hierarchical relationships in this species seem to be more relaxed and tolerant compared to other species (Norscia and Palagi, 2015). Even though agonistic interactions are used to determine ranks within groups, they are very rare (study II; Kappeler et al., 2009; Wheeler et al., 2013), seldom result in severe wounding and there are no reports of lethal aggression during fights in this species (Benadi et al., 2008). Also, lemurs in general use unidirectional vocal or olfactory signals to settle and assure their relationships (Benadi et al., 2008; Gould and Overdorff, 2002; Kappeler, 1998; Kulahci et al., 2015). In Verreaux's sifakas, rates of submissive chatter vocalisations are positively linked to grooming rates and negatively linked to rates of aggression (Lewis, 2019). Similarly, they use scent-marking, i.e. rubbing their anogenital and, in the case of males, sternal scent glands against the bark of trees, to regulate their relationships and communicate their presence (Benadi et al., 2008;

Lewis, 2005). Hence, the use of non-physical communication may mitigate the necessity of agonistic interactions (Flack and Waal, 2007).

Moreover, dominant males mate-guard females (Brockman, 1999; Mass et al., 2009) but mate-guarding is not associated with increased aggression, body size or weaponry (Lawler et al., 2005; Mass et al., 2009). Instead, males seem to rely on morphological traits which provide advantages in form of speed and agility during agonistic chases to increase reproductive success (Lawler et al., 2005). Female competition is ubiquitous - and a likely cause for Verreaux's sifakas' small group sizes (Kappeler and Schäffler, 2007; Steenbeek and van Schaik, 2001) - but relatively peaceful, since evictions have never been observed in this study population (Kappeler and Fichtel, 2012). Additionally, food competition is expected to be low due to sifakas' small group sizes and mainly folivorous diet (Janson and Goldsmith, 1995; Koenig, 2002). All these factors indicate that Verreaux's sifakas do not require frequent aggressive behaviours to compete with their group mates, because competition is low and they use other forms of communication to convey their social status and relationships and thus, avoid costly physical conflict.

Similarly, intergroup aggression in Verreaux's sifakas is moderate (Benadi et al., 2008; Koch et al., 2016b). Sifakas are territorial and defend their home ranges with both sexes participating in encounters (Jolly, 1966; Kappeler et al., 2009b; Koch et al., 2016b). Encounters between neighbouring groups are common and mostly occur at shared feeding sites in overlapping areas of their home ranges (Benadi et al., 2008; Koch et al., 2016a). Physical fights are, however, rare and animals usually use chases, stares, growls and scent marks during encounters (Brockman et al., 1998; Norscia et al., 2009). Moreover, the risk of group takeovers by external males is relatively low with 0.6 population-wide takeovers per year (Kappeler et al., 2009b) and infanticide is rare (Lewis et al., 2003b). A prior study in this population found that groups will not change their ranging and activity patterns when approaching overlapping home range areas, where the likelihood of encounters increases (Benadi et al., 2008). Hence, the risk of intergroup encounters does not exert changes to their behaviours – potentially because the costs of encounters are usually low.

Low rates of aggressive conflicts may also derive from Verreaux's sifakas' arboreal lifestyle. Arboreal species are characterised by less frequent agonistic interactions than terrestrial species (DeVore, 1963; Wheeler et al., 2013). This could be a result of the generally smaller group sizes found in arboreal species (Clutton-Brock and Harvey, 1977) in which competition over resources is considered reduced (Janson and Goldsmith, 1995; Janson and van Schaik, 1988). Another suggestion was that agonistic interactions on arboreal substrates involve higher energetic costs and are more risky in light of the danger of injury from falling (Hill and Okayasu, 1995). The complexity of the arboreal environment may also prevent animals from engaging in physical conflict, simply because it is too difficult to reach the opponents (Wheeler et al., 2013).

Altogether, Verreaux's sifakas mainly pursue non-violent, low-risk strategies to cope with inter- and intragroup competition. Rare aggressive interactions might derive from low within- and between-group competition per se and the high energetic costs and risks associated with physical conflict. Here, fGCM concentrations were not linked to aggressive behaviours (study II), indicating that Verreaux's sifakas' agonistic behaviours do not inflict high energetic constraints on individuals, and might thus not result in significant health-related consequences.

Moderate Affiliation = Moderate Health-Consequences?

Allogrooming is one of the most common affiliative behaviours in primates (Dunbar, 1991; Russell and Phelps, 2013) and other mammals (Kutsukake and Clutton-Brock, 2006; Stopka and Graciasová, 2001). This behaviour most likely evolved for hygienic functions, i.e. the removal of dirt and ectoparasites from hard-to-reach areas (Grueter et al., 2013; Hutchins and Barash, 1976). Allogrooming can also provide other health-related benefits, in terms of decreased heart rates (Aureli, 1997; Boccia et al., 1989) and increased insulation of animals' furs providing thermal benefits (McFarland et al., 2016), and it is associated with changes in concentrations of GCs (Crockford et al., 2008; Wittig et al., 2008) and oxytocin (Benítez et al., 2018). Frequent grooming of conspecifics serves the formation and maintenance of social relationships as shown in studies across different taxa (Kutsukake and Clutton-Brock, 2006; Madden and Clutton-Brock, 2009; Radford and Du Plessis, 2006; Sánchez-Villagra et al., 1998). In contrast to anthropoid primates, lemurs groom each other orally with so-called "toothcombs", a modification of the lower incisors and canines (Barton, 1987; Eaglen, 1980), which might facilitate the transmission of pathogens (Clough et al., 2010). On the other hand, allogrooming occurs at much lower rates in lemurs than in other primates (Sussman and Garber, 2004), which might limit opportunities for social transmission.

Several studies have established that Verreaux's sifakas exhibit low intestinal parasite diversity (Loudon and Sauther, 2013; Muehlenbein et al., 2003; Springer and Kappeler, 2016) and here, I found the same pattern (study I). Sifakas' arboreality and folivory might protect them from parasites that are transmitted via soil or use invertebrates as intermediate hosts (Loudon and Sauther, 2013; Springer and Kappeler, 2016). Animals may also utilize self-medication via the ingestion of certain plant species and soils (Huffman, 1997; Semel et al., 2019). Self-medicating behaviours are common in primates and, amongst other beneficial effects, may enhance parasite immunity (Carrai et al., 2003; Huffman, 2003; Peckre et al., 2018). Moreover, GI parasite diversity may also be inhibited if there are limited opportunities for social transmission between animal hosts. Allogrooming can function as an important driver for the transmission of GI nematodes (Friant et al., 2016; MacIntosh et al., 2012). However, Verreaux's sifakas devote little time to affiliative interactions, like allogrooming (studies II & III; Lewis, 2010, 2008), which could further contribute to their low nematode diversity.

It should be noted though, that the impact of social transmission of different microorganisms depends on their biological characteristics and modes of transmission. For example, the transmission routes of lemur-parasitising members of *Trichostronylidae* – which were present in all individuals (study I; Springer and Kappeler, 2016) – are still unknown (Irwin and Raharison, 2009). Larvae of *Trichostrongylidae* usually hatch in the environment and need several days to develop into an infective stage (Bush et al., 2001). Yet, Verreaux's sifakas are arboreal and spent very little time on the ground, providing few chances for picking up larvae. Faecal-oral transmission of this parasite, by which infective larvae cling to animals' furs and get swallowed by groomers during grooming bouts, might explain its high prevalence (Springer and Kappeler, 2016). Similarly, there are indications for social transmission of microbes in this species, as group members share the same *E. coli* strains (Springer et al., 2016) and groups harbour distinct gut bacterial microbiota (study III; Perofsky et al., 2017; Springer et al., 2017). However, neither the routes transmission nor the conditions necessary for the spread of microorganisms are well understood (Brito et al., 2019; Kuthyar et al., 2019; Robinson et al., 2019; Webster et al., 2017). Successful transmission might crucially depend on the duration of social contacts or external environmental conditions, e.g. temperature or humidity, (Browne et al., 2017; Ferguson and Signoretto, 2011; Rossanigo and Gruner, 1995; Sutherst and Bourne, 2006), which is why future research should address these important issues.

Ectoparasites usually require direct host-to-host contact for transmission and can be removed via auto- and allogrooming (Akinyi et al., 2013; Hawlena et al., 2007). Verreaux's sifakas harbour different ectoparasitic species, including mites, lice and ticks (Rasambainarivo et al., 2014; Springer, 2015). Prior research in this study population found ectoparasites mainly in regions that are difficult to groom, like armpits, ears or skinfolds, indicating that auto- or allogrooming may have removed parasites from other body parts (Springer, 2015). However, the same study did not detect links between allogrooming or body contact rates and the probability of ectoparasite infections. Thus, Verreaux's sifakas' short and relatively few allogrooming bouts may alleviate groomees from some ectoparasitic loads but are not sufficient enough to reduce ectoparasitic infection probabilities. Behavioural observations in this species are conducted during the day since sifakas are exclusively diurnal (Erkert and Kappeler, 2004). Yet, inclusions of body contact rates during the night might reveal new insights on the parasite spread. Especially during cold nights, group members huddle together for thermoregulation, which may provide sufficient host-to-host contact for ectoparasitic transmission throughout the groups.

Overall, allogrooming seems to have limited effects on sifakas' hygiene and health, but carries out important social functions as it helps maintaining group cohesion (Lehmann et al., 2007), enables sifakas to reassure their rank positions and relationships (Lewis, 2010), facilitates male mating success (Norscia et al., 2009) and is used by immigrants to negotiate group membership (Lewis, 2008). Considering its importance for sifakas' social life, why do they invest so little time in this behaviour?

Are Sifakas Too Busy or Too Scared to Groom?
- Impacts of Folivory and Predation Risk

Affiliative interactions can be time-consuming (Caraco, 1979; Korstjens et al., 2006; Pollard and Blumstein, 2008). Time is a finite resource and how much of this resource can be allocated to sociality depends on animals' habitats, diets and life history strategies (Dunbar et al., 2009; Marty et al., 2019). Folivorous species require longer resting times to allow for the digestion of leaf material (Fleagle, 2013; Korstjens et al., 2010; Pollard and Blumstein, 2008), resulting in less time available for social interactions (Kavana et al., 2015; Saj et al., 2007). Verreaux's sifakas spent the largest proportions of their days resting (47% study I) and foraging (45% to 47% study I & in Koch et al., 2017). During the study period, animals' foraging rates decreased slightly during the dry season and the time spent resting increased. However, in a prior study, the opposite patterns were found, yet, also here differences were small (Koch et al., 2017). Overall, feeding and resting durations in this species seem to be fairly stable throughout the year. Allogrooming rates in Verreaux's sifakas are unaffected by seasonality as well (Lewis, 2010). Over the course of the dry season, Verreaux's sifakas lose significant amounts of body mass and fat due to the increased energetic constraints caused by decreased food availability (Lewis and Kappeler, 2005) and higher needs of thermoregulation during cold nights. To cope with the challenges of the harsh dry season, sifakas store nutrients and fat, which need to be accumulated during the wet season (Koch et al., 2017). Such storing capacities have also been described in co-resident species, i.e. folivorous red-tailed sportive lemurs (*Lepilemur ruficaudatus*) (Ganzhorn, 2002), grey mouse lemurs (*Microcebus murinus*) (Schmid and Speakman, 2000) and fat-tailed dwarf lemurs (*Cheirogaleus medius*) (Dausmann, 2014). Verreaux's sifakas might, therefore, be obliged to spend the majority of their time foraging and resting throughout the year and regardless of whether food availability is high or low, in order to fulfil the energetic requirements of their challenging environment. Animals' may thus simply be too "busy" and unable to afford the time for extended sessions of allogrooming.

Additionally, grooming activities distract animals from being vigilant (Maestripieri, 1993) which can increase predation risks (Cords, 1995; Hart et al., 1992; Mooring and Hart, 1995). Oral grooming, in contrast to manual grooming, might put the individuals even more at risk, as they are not just distracted from their surroundings but their field of vision during grooming is also considerably impaired by the groomees' body. Predation pressure is generally high in lemurs since they represent the largest and most abundant mammals on Madagascar (Scheumann et al., 2007; Wright, 1998). In fact, the main cause of death in Verreaux's sifakas of Kirindy Forest, but also in other sifaka species, is fossa predation (*Cryptoprocta ferox*) (Kappeler and Fichtel, 2012; Pochron et al., 2004; Wright et al., 1997). Therefore, allogrooming, next to being time-consuming, also poses a source of danger for individuals and might thus not be conducted longer than necessary for maintaining social cohesion.

Energetic Constraints Shape Verreaux's Sifakas' Social Life

During the 2-year study period, all Verreaux's sifakas of the study population seemed to be "healthy" in the sense of the applied definition by Huber et al. (2011) (i.e. health is "the ability to adapt and to self-manage' when facing physical, mental, and social challenges") and no individual or group stood out in its behavioural patterns or physiological measures. All animals were able to do so despite living in a harsh and unpredictable environment, where they have to maintain core body temperatures, fight parasitic infections, find enough food and produce offspring. These requirements are energetically costly and might compromise animals' condition, especially in habitats where resources are limited. In comparison to haplorhines, lemurs have lower basal metabolic rates (Genoud, 2002; Simmen et al., 2010), which suggests that they rely on thermoregulatory behaviours to deal with the thermal stress during colder seasons. Smaller lemurs (< 200g body mass) usually enter daily torpor or hibernate (Dausmann, 2014), whereas larger lemurs will sun-bask and perform "social thermoregulation" by huddling together (Eppley et al., 2017a; Morland, 1993; Ostner, 2002). Verreaux's sifakas had increased fGCMs concentrations during the colder dry season in both study years (study II). This result supports the notion of increased energetic constraints during this time, which sifakas counter with reduced activity (study I; Erkert and Kappeler, 2004) and group-huddling.

Altogether, Verreaux's sifakas constantly face ecological challenges in form of food deprivation, high predation risks and thermal stress, which they manage to overcome by living in permanent association with conspecifics. However, their energetically demanding lifestyle and habitat appear to mainly constrain them from physical social interactions that go further beyond the maintenance of group cohesion. Health-related consequences of sociality are often related to increased stress through social conflict or isolation, which can increase susceptibility to diseases (Cohen, 2004; Kappeler et al., 2015) and to the increased transmission of pathogens (Freeland, 1976) and microbes (Lombardo, 2008; Turnbaugh et al., 2009). Here, I did not detect an effect of social relationships on animals' physiological conditions (study II & III), likely because of sifakas' low interaction rates and relaxed competition. Proximity to group members, however, was linked to gut microbial similarity (study III) and might facilitate the transmission of certain endo- and ectoparasites (study I; Springer and Kappeler, 2016).

Overall, I did not observe any signs of sickness or impaired health among the individuals, but it should be considered that my findings are based on non-invasive physiological parameters derived from faecal samples. Such measures provide valuable insights into animals' metabolic functions and general condition but cannot keep up with the accuracy and comprehensiveness of clinical studies. My study provides new evidence for the interplay of sociality, ecology and health in an endangered primate species but also underlies the typical constraints and limitations of field research, which I will briefly discuss in the following section.

5.3 Measuring Health in the Wild

Strengths & Limitations

Wildlife studies are important for investigations of the sociality-health nexus as they account for naturally occurring variation in aspects of sociality within an ecologically meaningful context. The inclusion and consideration of ecological and potentially confounding factors in my analyses proved very helpful for the interpretation of my results. For example, I provided evidence that fGCM concentrations are poor indicators for assessments of social stress in the wild, whereas they offer valuable insights into the energetic constraints animals face in their habitats, e.g. through changes in temperatures and food availability or gestation (study II). Due to the 2-year duration of the study, I could show recurrence of seasonal patterns in physiological adaptations and challenges. Next to the seasonal variation in fGCMs, I found nematodes of the family *Oxyuridae* to only occur during the wet season in both study years (study I) and detected consistent shifts in the abundance of certain gut bacterial phyla during the transition from the early to the late dry season (study III).

All physiological measures I used to investigate animals' health are derived from faecal samples, which are commonly utilised in field studies since they can be collected easily, non-invasively and repeatedly from the same individual (Touma and Palme, 2005). Nevertheless, faecal samples can only provide a glimpse on animals' physiological condition and there exist numerous confounding factors that can affect the results of their analyses.

Hormones

Faecal hormone metabolite (FHM) analyses enable the assessment of various endocrine functions and reflect the accumulated production rate of hormones over several hours (Touma and Palme, 2005). Endocrinological measures derived from faecal samples are mostly restricted to thyroid and steroid hormones, either because metabolites of other hormones are not secreted into faeces or they are too degraded for reliable detection (Behringer and Deschner, 2017; Pribbenow et al., 2017). There are numerous confounding factors which can influence FHM analyses, including study species, sex, diet, age or prenatal stress (Palme, 2019). Similarly, contamination with urine, water or blood can falsify measurements (Bahr et al., 2000; Behringer and Deschner, 2017). One of the most commonly utilised methods for measuring FHMs are immunoassays, which were also applied in this study. Importantly, there remains uncertainty about the metabolites which are picked up and measured with these assays due to the risk of cross-reactivity of the antibody (Goymann, 2012; Touma and Palme, 2005). Until these uncertainties are eliminated, results and patterns of FHMs derived from immunoassays should be interpreted with caution. Nevertheless, if methods for FHM analyses are correctly selected, validated and applied they can provide powerful tools for monitoring hormonal activity in wildlife.

Intestinal Parasites

The most commonly used methods to non-invasively quantify intestinal parasite burdens are estimations of prevalence and intensity via microscopy. However, identification and distinction of certain parasite species can be difficult due to morphological similarities (Polderman and Blotkamp, 1995). Here, I applied a metabarcoding approach by which I assessed parasite infestations using next-generation sequencing of 18S rRNA genes (Hadziavdic et al., 2014). To date, only a handful of studies have this approach to non-invasively assess intestinal parasites in animals (Avramenko et al., 2015; Srivathsan et al., 2016; Tanaka et al., 2014; Wimmer et al., 2004). Metabarcoding can facilitate differentiation among closely related species and constitutes a faster and more precise method in comparison to traditional analyses (Aivelo et al., 2018). Still, there is room for improvement since only a minority of parasite species is represented in reference databases and therefore detectable (but see Aivelo and Medlar, 2017; Wilson et al., 2011). My results on intestinal nematode infections in Verreaux's sifakas support the findings of prior studies (Loudon and Sauther, 2013; Springer and Kappeler, 2016), yet, more studies are required to complement the databases and reveal potentially unknown parasites.

Gut microbial analyses

There is an increasing number of wildlife studies investigating links between sociality and gut microbiota (Amato, 2016; Theis et al., 2012; Tung et al., 2015; Youngblut et al., 2019). However, even though our understanding of microbial communities has greatly improved within the past decade, we still know very little about microbiomes. To date, a large diversity of microorganisms remains completely unknown - occasionally referred to as "microbial dark matter" (Bernard et al., 2018; Thomas and Segata, 2019) -, we are just beginning to identify the factors that influence gut microbiota and our insights into the functions and transmission routes of bacteria are limited (Browne et al., 2017; Moeller et al., 2018; Rinninella et al., 2019). Thus, there is much more work required before we can fully understand the impact of gut microbial communities on animal and human health. More basic research should be implemented in future research (e.g. by examining hourly and daily shifts in microbial compositions) and future studies need to acknowledge the limited insights and myriads of unanswered question concerning this field of research to avoid mis- and over-interpretation.

Future directions

Here, I provide comprehensive research on associations between different aspects of group living and measures of fGCM concentrations, parasite richness and gut microbiota in wild Verreaux's sifakas. However, the links between sociality and health are complex and there remain many unanswered questions that need to be addressed in future studies. A well-functioning immune system is necessary for pathogen resistance and ultimately for survival. There exist a range of non-invasive immune markers derived from faecal or urinary samples (Higham et al., 2015), which could be implemented in future

research and would provide valuable information on individual immune responses, especially in combination with endocrinological parameters and assessments of gut microbial communities. Further investigations in this species should also relate measures of health to long-term data on survival and reproductive success to assess the fitness consequences of individual variation in health that derived from the evolution of group living.

5.4 Conclusions

A Small Step Closer Towards Understanding the Evolution of Sociality

The transition from solitary to group living yielded various new health-related costs and benefits. However, the magnitude of these health consequences may depend on species-specific aspects of their sociality, i.e. social organisation, social structure and mating system (Kappeler and van Schaik, 2002). Individuals living in highly competitive societies may be exposed to higher rates of agonistic and affiliative interactions, which represent a source for variation in physiological or psychological stress and can increase opportunities for transmission of pathogens and microbes. On the contrary, in species with less competitive regimes and low interaction rates, health-consequences of sociality might be attenuated. Here, I only found few implications for health-related consequences of group living in Verreaux's sifakas, potentially reflecting the species' low competition within and between groups, little investment in social relationships and avoidance of physical aggression. Importantly, I found strong impacts of environmental factors on animals' behaviours and physiology which might have obscured patterns of the sociality-health nexus, underlying the importance of examining the nexus within an ecologically meaningful context.

There is still little understanding of the complex and interrelated factors that contribute to the sociality-health link and its consequences for individual fitness. Future research should comprise of comprehensive wildlife studies in species with different social systems. In light of the rapid advances on applications of non-invasive techniques to field studies and the constant progress in molecular and statistical methods, upcoming research holds great potential for providing major contributions to the understanding of the co-evolutionary dynamics and factors that shaped the evolution of sociality.

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Acknowledgements

As the successful completion of such a dissertation is also depending on the cooperation of others. I would like to thank those who enabled me to accomplish this work.

First, I would like to express my sincere gratitude to Dr. Claudia Fichtel and Prof. Peter M. Kappeler for their academic supervision, their constructive feedback and for giving me the incredible opportunity to work with wild lemurs in Madagascar!

I am grateful to Dr. Michael Heistermann for welcoming me into his Endocrinology Lab and for his patience and support during hormone analyses. Special thanks also to Andrea Heistermann and Miriam Bolte for being there whenever I had questions and for their entertaining stories during long hours of diluting samples. It was truly a pleasure to work with all of you!

Thank you very much Dr. Dominik Schneider for introducing me to your weird world of bacteria, dirt and "fairy water". You were always patient and understanding of my microbial unknowingness and eventually even managed to get some microbial wisdom into me!

I am thankful to Prof. Julia Ostner and Prof. Rolf Daniel for being part of my thesis committee and for bringing new perspectives and ideas to my project. I also want to thank Dr. Dietmar Zinner and Prof. Lars Penke for agreeing to be part of my examination board.

Without the help of Tianasoa Andrianjanahary and Mamy Solohery Razafindrasamba and the other assistants at the field station in Kirindy Forest, this work would not have been possible. Thank you very much!

I am grateful to all past and present members of the Behavioral Ecology and Sociobiology Unit of the German Primate Center and to all the members of the Research Group "Sociality and Health in Primates" for numerous fruitful discussions during retreats, workshops and coffee breaks. A huge thank you goes to Johanna Henke - von der Malsburg for the many fun hours inside and outside of our office and for your very helpful comments and suggestions on this thesis.

Many final thanks go to my family and friends for their unfailing confidence and support.

Declaration

I hereby declare that all parts of my thesis titled **"Health consequences of group living in wild Verreaux's sifakas (*Propithecus verreauxi*)"** were written by myself. Assistance of third parties was only accepted if scientifically justifiable and acceptable in regard to the examination regulations. Assistance or contributions to the individual chapters are indicated and all sources have been quoted.

Göttingen, 19th of December 2019

Katja Rudolph