Behavioral and Feeding Ecology of a Small-bodied Folivorous Primate (*Lepilemur leucopus*)

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SUMMARY

Small-bodied folivorous primates are rare because processing leaves often requires extensive gut adaptations and lengthy retention times for fiber fermentation. However, *Lepilemur leucopus* (white-footed sportive lemur) persists on a folivorous diet despite small body size (<1kg). To improve our knowledge about how small-bodied folivores adapt their behavioral and dietary strategies to satisfy their nutritional needs, I aimed to investigate how extrinsic (i.e. food quantity and quality) and intrinsic (i.e. reproductive state) factors influence foraging strategies, food choices and social relationships. I collected data on activity patterns, feeding behavior, social interactions and ranging behavior in a spiny forest population of *L. leucopus* at Berenty Reserve, Madagascar, over a complete annual cycle. I determined habitat structure and phenology of the spiny forest and collected foods for chemical analyzes of nutritional content. There was no consistent evidence that the seasonal decrease in food quantity had a major impact on feeding behavior or social interactions in *L. leucopus,* presumably due to its low dietary selectivity and reliance on the most common food species, and any feeding stress may have been more related to food quality than quantity. In more particular, dietary protein may have been in limited supply as *L. leucopus* prioritized protein over non-protein intake across seasons and reproductive stages. As changes in activity patterns and social interactions were unrelated to food quantity, bottom-up processes seem to be less important than top-down processes in shaping the social system of *L. leucopus.* The findings also support the idea that quantitative food shortage during the dry season may be subordinate to leaf quality as a selection pressure on folivorous primate populations.

ZUSAMMENFASSUNG

Kleine blattfressende Primaten sind selten, da die Verarbeitung von Blättern oft umfangreiche Anpassungen des Verdauungsapparates und lange Retentionszeiten für die Fermentierung der Blattfasern erfordert. Dennoch basiert die Nahrung von *Lepilemur leucopus* (Weißfuß-Wieselmaki) auf Blättern trotz kleinem Körpergewichts (<1 kg). Um unser Verständnis darüber voranzutreiben wie kleine Blattfresser ihre Verhaltensstrategien anpassen um ihre Nahrungsbedürfnisse zu stillen, beabsichtigte ich zu untersuchen wie extrinsische (i.e. Nahrungsquantität und -qualität) und intrinsische Faktoren (i.e. Fortpflanzungsstatus) Strategien der Nahrungssuche, Nahrungswahl und soziale Interaktionen beeinflussen. Ich sammelte Daten bezüglich Aktivitätsmuster, Fressverhalten, sozialer Interaktionen und Streifverhalten in einer Population von *L. leucopus* in Berenty Reserve (Madagaskar) über einen kompletten Jahreszyklus. Ich erhob Daten zur Habitatstruktur und Phänologie des Dornenwaldes und sammelte Blattproben für die chemische Analyse des Nährstoffgehaltes. Es gab keine eindeutigen Anhaltspunkte, dass die saisonale Abnahme in der Nahrungsverfügbarkeit einen beträchtlichen Einfluss auf Fressverhalten oder soziale Interaktionen in *L. leucopus* hatte, vermutlich aufgrund der geringen Nahrungsselektivität und der Nutzung der am häufigsten im Wald vorkommenden Pflanzenarten, und Nahrungsstress stand wahrscheinlich eher mit Nahrungsqualität als -quantität in Verbindung. Nahrungsprotein scheint nur begrenzt zur Verfügung gestanden zu haben, da *L. leucopus* Protein- gegenüber nicht-Protein-Aufnahme über Jahreszeiten und Reproduktionsstadien hinweg priorisierte. Da Veränderungen hinsichtlich Aktivitätsmuster und sozialer Interaktionen nicht im Zusammenhang mit Nahrungsknappheit standen, scheinen Bottom-Up-Prozesse weniger wichtig als Top-Down-Prozesse für die Formgebung des sozialen Systems von

L. leucopus zu sein. Die Ergebnisse unterstützen außerdem die Idee, dass quantitative Nahrungsknappheit während der Trockenzeit eine untergeordnet Rolle gegenüber Blattqualität als Selektionsdruck für blattfressende Primatenpopulationen spielt.

GENERAL INTRODUCTION

Nutrition is the basis for all life processes as it delivers energy for maintenance, growth and reproduction. As diet is related to almost all aspects of behavior, morphology, and physiology, it is a central component of a species' biology. Moreover, a species' feeding ecology relates to its life history, population dynamics, habitat requirements, and patterns of sociality (Robbins and Hohmann 2006). Furthermore, studies of the chemical basis of food choice further our understanding of foraging strategies and dietary decisions (Whiten et al. 1991), of the ecological basis of variation in social organization (Byrne et al. 1993), and of the determinants of animal abundance (Chapman et al. 2002).

In general, the rate at which an individual can acquire energy and nutrients depends on the quantity and quality of the available food resources, and foraging behavior can be considered successful only if the diet obtained provides sufficient amounts of energy and nutrients to fulfill the energetic and nutritional requirements of the forager (Oftedal et al. 1991). The rate of energy gain and nutrition of an individual is influenced by several factors such as a.) species-specific diet, b.) seasonal variation in the quantity, quality and distribution of food resources, c.) sex-specific differences in energetic needs due to differing costs of reproduction and d.) the presence of other individuals that compete for the same food resources.

In this general introduction, I will provide more details on each of these factors. Subsequently, I will outline why the white-footed sportive lemur (*Lepilemur leucopus*) constitutes a suitable study species. Finally, I will highlight which aspects of the behavioral and feeding ecology of *L. leucopus* I explored in each chapter of this thesis and which approaches I used to do so.

Species-specific diet

Primates are able to exploit a wide range of food sources such as fruits, leaves, flowers, seeds, insects or gums. Therefore, individual species are often referred to as predominantly frugivorous, insectivorous, gummivorous or folivorous according to the dominant type of food, and dietary adaptations can be related to the structural and biochemical features of their food sources (Lambert 1998). Although large animals have higher absolute metabolic requirements than small animals, they actually require less energy intake per unit of body weight. Therefore, large animals are able to subsist on abundant low-quality foods, whereas small animals tend to concentrate on relatively rare foods of high quality (Gaulin 1979). The major food type of small primates tends to be invertebrates, whereas fruits, seeds or gum are usually the principal foods of medium-sized species. In contrast, larger species rely on leaves as the major food source (Hladik 1979).

The diet of insectivorous primates is high in protein, energy and is easy to digest (Schmidt-Nielsen 1997). However, insects are often scarce food items as they are small in size, very seasonal and less abundant than leaves and fruits. Whereas fruits are a source of readily available energy as they contain ample sugar, frugivorous primates supplement their diet with insects and young leaves to acquire protein (Janson and Chapman 1999). Folivorous primates subsist on a diet that can be considered to be of low quality as leaves are a poor source of readily available energy. They are generally high in difficult to digest structural carbohydrates. In order to extract energy from a highly fibrous diet, fermentation of ingested plant food has to take place (Milton 1993).

As an adaptation to their diet, folivorous species have a complex stomach (in primates only found in colobines) and/or an enlarged cecum and colon (in some species of strepsirrhines, New World monkeys, cercopithecines, and hominoids) in order to increase the total amount of food that can be consumed in one session, and to allow for enough time for bacteria to break down secondary compounds and cellulose (Lambert 1998). For folivorous species it is advantageous to have a large body size as larger gastro-intestinal surface area and longer digestion time allow maximum nutrient absorption (Chivers and Hladik 1980). However, folivory is also observed in some small-bodied (i.e. < 1kg) primate species such as woolly lemurs (*Avahi* spp.) and sportive lemurs (*Lepilemur* spp.). Whereas the relative energy requirements increase with decreasing body size, little is known about whether or how these can meet their energy requirements through diet selection.

Seasonality

Seasonal climate variability affects the life of animals indirectly through its effect on the phenology of the plant community, thus resulting in seasonal changes in the abundance, nature and distribution of potential food items (van Schaik and Brockman 2005). Reduced food quality/quantity during the dry season can be expected to influence behavior and feeding strategy of primates. The effects of seasonality have been rarely studied in folivorous primates, as leaves were often thought of as a resource in constant supply. However, it has been shown that primates prefer young over mature leaves (Chapman et al. 2004), and that the amplitude of leafing seasonality can be greater than that of fruiting (Hemingway 1998). Furthermore, folivorous primates are more tightly linked to primary production and thus are regulated more by bottom-up processes than other species that forage at higher trophic levels (e.g. insects; Ganzhorn et al. 2003).

There is a controversy about which seasons and what factors can be considered as limiting for primate populations (Ganzhorn 2003). However, an understanding of these factors will further our understanding of how ecological factors influence primate distribution, community structure and social systems (Ganzhorn 2002). While the abundance of fallback foods (e.g. figs) during periods of food scarcity may limit populations of frugivorous primates (Marshall and Leighton 2006; Potts 2009), the abundance of preferred foods (i.e. leaves of high protein to fiber concentration) during periods of food abundance seems to limit populations of folivorous primates (Ganzhorn 1992, 2002; Chapman et al. 2002). In any case, primates should have evolved adaptive strategies such as dietary, ranging and/or physiological adaptations to overcome periods of food scarcity in seasonal environments (Hemingway and Bynum 2005).

Dietary adaptation in response to food scarcity can occur in the form of switching between food categories (e.g. leaves, fruits etc.), switching to a different item within a food category (e.g. different fruit species) and concentrating feeding efforts on a smaller number of critical food resources (Hemingway and Bynum 2005). Most studies of primate diets determine the relative contribution of different food types rather than analyzing the nutrient composition of specific food items. However, animals require a wide range of nutrients (carbohydrates, fats, proteins, vitamins and minerals) for body maintenance (National Research Council 2003), and no single food type can be expected to provide a species with a fully balanced diet. The Geometric Framework for nutrition allows assessing the influence of seasonal changes in food availability and quality on nutritional intake patterns (Simpson and Raubenheimer 1993).

Reproductive investment

Many factors may affect sex differences in feeding ecology and activity budgets in primates and can be attributed mainly to sexual dimorphism, to avoidance of competition between the sexes and to variation in costs of reproduction. Whereas differences in body size affect the amount of food that an individual requires (Kamilar and Pokempner 2008), dietary differences can lead to competition avoidance between sexes and therefore, can be considered adaptive for males and females (Selander 1972). Furthermore, whereas females bear the energetic costs of gestation and lactation (Gittleman and Thompson 1988), males bear the cost of male-male competition (Lane et al. 2010; Schubert et al. 2009b). Individuals can be expected to compensate for increased energetic demands by eating higher quality or more food or by other behavioral means.

In monomorphic species energetic costs of body maintenance should be similar for males and females. Therefore, the overall energetic costs are likely to be greater for females who bear the costs of pregnancy and lactation in addition to the costs of body maintenance (Key and Ross 1999). Lemurs (Lemuriformes) provide a special opportunity to test hypotheses concerning sex differences due to their body size monomorphism (Kappeler 1991). Sex-specific differences in activity patterns (Schmid 1999), diet (Grassi 2002; Vasey 2002), ranging behavior (Kappeler 1997) and habitat-use (Vasey 2002) have been shown for several lemur species. However, few studies have directly linked these differences to sex-specific reproductive costs or energy expenditures (see e.g., Rothman et al. 2008; Gould et al. 2011).

Seasonal breeding is a typical lemur trait (Rasmussen 1985; Petter-Rousseaux 1980) and can be seen as an adaptation of species residing in habitats with pronounced seasonal fluctuations of food resources (Janson and Verdolin 2005), as females can enhance their overall fitness by coordinating costly times of reproduction with times of increased energy availability in order to compensate for peaks in energy expenditure (Sadleir 1969). Females experience an increase in energetic costs by up to 25 and 50% during gestation and lactation, respectively (Portman 1970). To meet increasing demands, lactating females must supplement their own nutritional intake. Lactating females may spend more time feeding (Koenig et al. 1997), and may consume a higher proportion of protein-rich foods (Sauther 1998) than males, non-reproductive females, or pregnant females (Sauther and Nash 1987).

As sexes differ in the quantity and composition of resources they require to maximize reproductive output, each sex should have different optimal nutritional intake targets, which can be evaluated by using the Geometric Framework for nutrition (Raubenheimer and Simpson 1997). Resource demands of offspring should alter the nutritional intake targets of reproductive females relative to males and non-reproductive females and these biases should become increasingly apparent as gestation and lactation progress (Morehouse et al. 2010). Although previous studies have demonstrated that males and females differ in their diets, they have rarely connected the compositional difference of ingested foods to sex-specific nutritional optima.

Feeding competition

Competition arises when individuals sharing the same environment depend on resources that are available only in limited amounts. Competition for food has fitness consequences, including increased mortality and lowered female reproductive success (Altmann et al. 1988; Dittus 1979; Martin and Martin 2001; Schülke 2003; Whitten 1983; Wittig and Boesch 2003). Competition for food can occur within or between social units and, depending on food abundance, quality and distribution (Isbell 1991), two modes of feeding competition can be distinguished (Nicholson 1954). When resources are dispersed, of low quality, or very large, scramble competition occurs as each individual in the population will indirectly reduce the net energy gain of all others in the population. When resources are medium-sized, of high quality or clumped in patches and can thus be monopolized, contest competition occurs as dominant individuals can constrain the net energy gain of subordinate individuals (Koenig 2002).

The various forms of food competition can be linked to the nature of social relationships within a social unit (van Schaik 1989; Sterck et al. 1997). Contest competition for food leads to despotic relationships between individuals of a group with higher-ranking individuals having priority of access to food. Behavioral consequences are direct contest over food and may take the form of aggression, displacement or avoidance. Subordinate individuals try to compensate this effect by feeding away from others on resources of similar quality or they may accept the losses and try to avoid aggression by feeding on resources of lower quality (Janson and van Schaik 1988). If scramble competition predominates, dominance relationships between individuals will be more egalitarian. Competition increases in intensity with group size and smaller groups are favored. Adjustments of ranging behavior to group size, including home-range size and daily travel distance, are thought to reflect scramble competition (Isbell 1991).

The socioecological model (Terborgh and Janson 1986) links ecological factors with characteristics of social systems and allows predictions about the relationship between resource distribution, type of competition and consequences for social organization (van Schaik 1989). Solitary individuals typically forage alone, but that does not mean that they do not maintain social relationships (Bearder 1987). Although nocturnal primates are often found alone, overlapping home ranges or territories ensure that conspecifics meet on a regular basis when a variety of social interactions occur (Bearder 1999). Previous studies of lemurs revealed that food competition does not only occur in group-living primates but also among solitary gummivorous and omnivorous foragers (Schülke 2003, Dammhahn and Kappeler 2009). The types and consequences of competition in solitarily foraging folivorous primates have not been studied in detail yet.

Why study sportive lemurs?

Primates present a promising taxon to conduct comparative studies on behavioral, feeding and nutritional ecology. On the on hand, they exhibit varying social systems and degrees of social cohesiveness (Kappeler and van Schaik 2002). On the other hand, their habitats differ in terms of resource abundance, climatic seasonality and predation risk (Wolfheim 1983). Such pronounced variability allows exploring ecological determinants of social relationships as well as nutrient requirements.

I chose *Lepilemur leucopus* (white-footed sportive lemur) as my study species for several reasons. It is one of the smallest folivorous primates and, therefore, should have evolved adaptive mechanisms to deal with a low quality diet. The highly seasonal, climatic unpredictable, arid southern domain of Madagascar with a short wet season provides an ideal background to study mechanisms with which primates adjust their behavior to varying ecological conditions such as seasonal resource bottlenecks. The pronounced seasonality also likely exacerbates the energetic costs of reproduction and thus promotes more pronounced sex differences (Sauther 1993). Like most lemurs (Kappeler 1991), *L. leucopus* lacks sexual size dimorphism, which allows the study of sex-specific costs and compensation strategies that are not complicated by sex-dependent variances in energetic requirements and behaviors due to differences in body size (e.g. Rodman 1977; Gautier-Hion 1980). In addition, like most lemurs, sportive lemurs breeds annually and seasonally (Randrianambinina et al. 2007; Hilgartner et al. 2008), so that each individual in a given study population undergoes the same seasonal or reproductive stages in tandem (Vasey 2005).

As sportive lemurs are characterized by a folivorous diet and small home ranges (approximately 0.3-1.2 ha; Thalmann and Ganzhorn 2003), a more precise measurement of food characteristics than for other species with larger home ranges and broader diets is facilitated (Ganzhorn 2003). This species also allows testing the types and consequences of competition in solitarily foraging folivorous primates. Direct behavioral observations are often limited by poor visibility conditions in arboreal primates (Nash 1998; Thalmann 2001). *Lepilemur leucopus* occurs in the spiny forests of southern Madagascar, a habitat that permits to observe the animals clearly and continuously, despite their nocturnal activity (Hladik and Charles-Dominique 1974).

Currently, 24 species of the genus *Lepilemur* are recognized (Ramaromilanto et al. 2009). Only two species, *L. ruficaudatus* (red-tailed sportive lemur) and *L. edwardsi* (Milne-Edwards' sportive lemur), have been studied in greater detail (e.g. Hilgartner et al. 2008; Ganzhorn et al. 2004; Mendez-Cardenas and Zimmermann 2009; Randrianambinina et al. 2007). The remaining species received only little scientific attention so that their diversity, distribution, and biology remain poorly known (Mittermeier et al. 2003; Mittermeier et al. 2010). Similarly, the only studies previously conducted on *L. leucopus* date back to the 1970’s and were of relatively short duration (2 and 4 months, respectively; Charles-Dominique and Hladik 1971; Hladik and Charles-Dominique 1974; Russell 1977). A more recent study on the behavioral ecology of the sportive lemurs of Southern Madagascar was conducted at Beza Mahafaly Special Reserve in a gallery forest habitat (Nash 1998). Formerly believed to belong to *L. leucopus*, this population at Beza Mahafaly is now considered to represent a separate species (*L. petteri*; Hoffmann 2008). As a collateral benefit to primatologists, this thesis contributes to our limited knowledge of the natural history of *Lepilemur* in general and *L. leucopus* in particular.

Background information on sportive lemurs

Sportive lemurs have evolved a number of adaptations to deal with constraints imposed by their comparatively low-quality folivorous diet. Amongst them are the elongated cecum (Tattersall 1982), one of the lowest basal metabolic rates among folivorous mammals (Schmid and Ganzhorn 1996) as well as extended nightly resting periods (Ganzhorn and Kappeler 1996). While some researchers have argued that this exceptionally small folivore couples hindgut fermentation with the reingestion of feces (i.e. cecotrophy; Hladik 1978), others have found no evidence of such behavior (Russell 1977). Together, these adaptations indicate that sportive lemurs are subjected to ecological constraints, however, it remains unclear how these affect their foraging strategies.

Only a few studies have addressed possible seasonal effects on *Lepilemur* behavior. *Lepilemur petteri* exhibits a unique pattern of not shifting its feeding time while trading off moving and resting time (Nash 1998). Therefore, it was hypothesized that *Lepilemur* eats as much as it can at all seasons, so that the only way it might conserve energy is to rest more, since it is constrained in its ability to acquire more energy. However, in order to test this hypothesis information on relative seasonal changes in food quality and quantity are needed. Furthermore, *Lepilemur ruficaudatus* was shown to adjust its home range to the presence of high quality leaves during the abundant wet season and, therefore, conditions during the wet season seem to be more important than during the dry season (Ganzhorn 2002). In contrast, Nash (1998) suggested that the coldest part of the year poses the greatest energetic stress for *Lepilemur*. It therefore remains unclear which season can be considered as energetic bottleneck.

Ganzhorn et al. (2004) could not find profound sex-specific differences in food selection in *L. ruficaudatus* during the wet season (corresponding to the time of lactation and weaning). However, their analyses were restricted to the average chemical composition of foods ingested and neither the amount of food ingested or the relative contribution of various food items was considered. Field metabolic rates measured in *L. ruficaudatus* did not differ between males and females (Drack et al. 1999). However, the study was restricted temporarily to the months of July/August (corresponding to the time of early gestation) and no information on the reproductive state of the females was provided. It therefore remains unclear how differing energetic cost of reproduction translate into sex-specific differences in food selection and energy expenditure.

Individuals of *Lepilemur* exhibit territoriality (Charles-Dominique and Hladik 1971, Zinner et al. 2003) and defend a space that includes potential food resources that provide nutrition throughout the year. The use of latrines has been noted in *Lepilemur* (Charles-Dominique and Hladik 1971; Russell 1977) and may be linked to resource defense (Irwin et al. 2004). Feeding competition has not been studied in *Lepilemur* so far and it is unclear how it influences the social organization of this solitary forager.

While dispersed pair-living has been described for *L. ruficaudatus* (Zinner et al. 2003) and *L. edwardsi* (Méndez-Cárdenas and Zimmermann 2009), two short field studies conducted on the same population of *L. leucopus* at Berenty Reserve in the 1970s reported conflicting patterns of social organization. While Charles-Dominique and Hladik (1971) proposed a “dispersed harem”, Russell (1977) reported coincidence and exclusive use of a range usually by two individuals.

Aims and approaches

The socio-ecological model describes the distribution of resources and risks in the environment as the main ecological factors shaping individual behavioral interactions (Jarman 1974; Terborgh and Janson 1986; van Schaik 1989) and identifying the relative importance of these bottom-up and top-down processes for the evolution and maintenance of social systems is a primary objective of behavioral ecology (Dammhahn and Kappeler 2010). Although leaves have traditionally been considered a rather invariant and abundant resource, more recently it has been shown that at least some folivorous primates experience behavioral and physiological effects of food limitation (Harris et al. 2009). This thesis was designed to add new insights into the mechanisms by which folivorous primates adjust to seasonally varying ecological conditions by studying a primate species in which diet-related constraints are likely exacerbated by small body size and pronounced climatic seasonality. Social and organizational features largely derive from food choices and dietary energetics (Hohmann et al. 2006) and by integrating research on behavioral and feeding ecology, I aimed to contribute to our knowledge of how bottom-up factors shape social systems of solitary foragers.

In **Chapter 1** I describe the social organization and the social structure of *L. leucopus* based on behavioral and ranging data I collected during a year-long field study in Southern Madagascar. By empirically identifying natural social units, quantifying the degree of cohesiveness within social units and reporting on patterns of social interactions within and between social units, I am laying the foundation for the subsequent chapter.

In **Chapter 2** I investigate the competitive regime of folivorous *L. leucopus* by describing the types of feeding competition between and within social units across a whole year encompassing an abundant wet and a lean dry season. In addition, I explore whether feeding competition may promote spatial avoidance and solitary foraging in folivorous solitary foragers and compare my findings with respect to other studies on gummivorous and omnivorous solitary foragers.

In **Chapter 3** I examine the function of latrine use, a special form of scent marking, in *L. leucopus* by investigating latrine distribution, seasonality of latrine use, as well as age and sex of users. Whereas it has been suggested previously that latrine use in sportive lemurs may be linked to resources defense such as of important food patches, I test this and other hypotheses empirically by detailing latrine density and distribution, seasonality and behavioral contexts of latrine use.

In **Chapter 4**, I analyze daily macronutrient and energy intake in male and female individuals of *L. leucopus* during different periods of the year in order to explore consequences of ecological and reproductive seasonality on nutritional intake targets. In addition, I explore how this small-bodied folivore can overcome energetic constraints imposed by a diet that constitutes a poor source of readily available energy.

CHAPTER 1

Defining the low end of primate social complexity: the social organization of the nocturnal white-footed sportive lemur (*Lepilemur leucopus)*

With Peter M. Kappeler

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Abstract

While other species of sportive lemurs (genus *Lepilemur*) have been described as living in dispersed pairs, which are characterized by spatial overlap but a lack of affinity or affiliation between one adult male and female, existing reports on the social organization of the white-footed sportive lemur (*Lepilemur leucopus*) are conflicting, describing them as either living in dispersed one-male multi-female systems or pairs. We conducted this study in the spiny forest of Berenty Reserve, southern Madagascar, to clarify the social organization and to characterize the level of social complexity of this species. We combined 1530 h of radio-telemetry and behavioral observations over a period of one year to describe the spatiotemporal stability, size and inter-individual overlap of individual home ranges as well as inter-individual cohesiveness. Results revealed low intra- and high intersexual home range overlap. While most of the social units identified consisted of dispersed pairs (N=5), males were associated with two adult females in two cases. Furthermore, members of a social unit were never observed to groom each other or to share a day-time sleeping site, and Hutchinson's and Doncaster's dynamic interaction tests indicated active avoidance between pair partners. Low cohesiveness together with extremely low rates of social interactions therefore arguably places *Lepilemur leucopus* at the low end of primate social complexity.

Introduction

The majority of primate field studies have been concerned with descriptions and analyses of their social systems (Crook and Gartlan 1966; Smuts et al. 1987; Mitani et al. 2012). There is an emerging consensus that the diversity of primate social systems can be analyzed at the level of their social organization, mating system and social structure (Kappeler and van Schaik 2002; Cords 2007; Kappeler et al. 2013). Interspecific variation in social systems has also been analyzed more recently as a function of social complexity (e.g., de Waal and Tyack 2003; McComb and Semple 2005; Bergman 2010; Lehmann and Ross 2011). In this context, complex social systems have been defined as those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals in networks over time (Freeberg et al. 2012). Social complexity is therefore an integrative measure that is positively correlated with group size because, according to the social intelligence hypothesis (Dunbar 1998), animals living in larger groups should have enhanced cognitive abilities to facilitate the management of multiple social relationships, compared to those living in smaller groups or in other types of social organization (Byrne and Whiten 1988; Bond et al. 2003; Dunbar and Shultz 2007). However, social complexity has not been explicitly studied in primates that do not live in groups, so that it is currently difficult to define a baseline for comparative studies of social complexity.

The absence of group-living among primates is strongly correlated with nocturnal activity (van Schaik 1983). Even though about a quarter of all primates are nocturnal, their social systems have remained comparatively poorly studied (Bearder 1999). Nocturnal primates have initially been collectively characterized as “solitary foragers” (Petter et al. 1977; Bearder 1987), but methodological advances in telemetry and molecular genetics have since disclosed more details of the diversity and complexity of their social systems (summarized in Nekaris and Bearder 2011; Kappeler 2012). In particular, some species of dwarf (*Cheirogaleus* spp.) and sportive lemurs (*Lepilemur* spp.) were found to be organized into pairs, even though individuals forage solitarily (Fietz 1999; Müller 1999; Rasoloharijaona et al. 2003; Zinner et al. 2003). Since pairs are the smallest social units, and pair-living requires active coordination between pair-partners (Schülke and Kappeler 2003; Barelli et al. 2008), and because its evolutionary emergence was associated with a significant increase in brain size (Shultz and Dunbar 2007), pairs represent an interesting level of analysis for comparative studies of social complexity. Species that combine aspects of the likely evolutionary transition between a solitary social organization and pair-living might be particularly interesting in this context because they may represent the earliest and most primitive form of sociality.

Our study focused on a species of sportive lemur for which conflicting information about the social organization of the same population had been reported. White-footed sportive lemurs (*Lepilemur leucopus)* are confined to the region between the Menarandra and Mandrare rivers in southern Madagascar (Hoffmann 2008). They have evolved adaptations to a folivorous diet despite small body size (< 1kg), including prolonged resting bouts, small night ranges, a prolonged cecum and cecotrophy (Hladik and Charles-Dominique 1974). Two short field studies were conducted on the same population of white-footed sportive lemurs at Berenty Reserve in the 1970s and reported conflicting patterns of social organization (Charles-Dominique and Hladik 1971; Russell 1977). Charles-Dominique and Hladik (1971) described exclusive range use by both sexes, but range overlap between the sexes, and found that the largest male was associated with five females. Russell (1977) reported that no individual had an exclusive range and described range-sharing by females. He also observed males and females sleeping together during the day. Based on these observations, the social organization of

L. leucopus has been classified as a “dispersed harem” (Müller and Thalmann 2000). Neither study used radio-tracking or detailed patterns of social interactions.

The present study aimed at resolving these conflicting reports by characterizing the social organization of *L. leucopus* during a year-long study of radio-collared individuals. In particular, we empirically identified natural social units and investigated their stability across the year in this seasonal breeder. In addition, we quantified the degree of cohesiveness within social units using three different computational approaches and report on patterns of social interactions within and between social units. Together, these data also contribute to our second aim, namely the characterization of the level of social complexity in this small nocturnal lemur.

Methods

Study site and subjects We conducted this study at Berenty (S 25.00°, E 46.30°), an approximately 200 km^2 private ecotourism reserve located in southern Madagascar. In order to ensure continuing focal observations of single individuals throughout the night, we equipped animals with radio-tracking transmitters. We captured the animals by blow-darting in a spiny forest fragment of about 5 ha (HAH Reserve Forestière parcel 1), which is connected to gallery forest on one side via a transitional forest and a further 40 ha spiny forest fragment on the other side (Norscia and Palagi 2008).

We used a blowpipe and 1 ml air pressured narcotic syringe projectiles (Telinject, Germany) to anesthetize animals with 0.4 ml Ketanest (100 mg/l) in the mornings in their daytime resting sites. We captured anesthetized animals with a blanket when they fell out of the tree. Alternatively, if the anesthetized animals did not fall and it was possible to reach them by climbing the tree, we retrieved them from their resting sites by hand or with an animal capture pole (Tomahawk 7’ to 12’ extension restraint pole). We fitted the animals with radio-collars (TW-3 button-cell tags, Biotrack, UK) while anesthetized. We kept the animals in an animal transport box (Traveller Box Capri Mini, Trixie Heimtierbedarf, 40*22*30 cm) until they were fully recovered and released them again at their capture site in the evening. The same individuals later reused sleeping trees where they were captured.

We fitted sixteen adult (eight males and eight females) and four subadult individuals (three males and one female) with radio-collars. We differentiated adult individuals from subadults by the degree of tooth wear and body mass. At the beginning of the study, all subadult individuals still ranged within their parental territories. Once they dispersed from their natal range, we classified them as adults. We did not radio-collar smaller juvenile animals because radio-collars exceeded 4% of their body mass. Some members of social units were not equipped with radio-collars. However, we noted their presence during animal capture, focal animal observations and a population census at the end of the study. We removed all radio-collars after the end of the study. The research followed standard protocols for animal handling, capture and radio-tracking and was approved by the Commission Tripartite CAFF (Madagascar).

Behavioral observations We collected behavioral and locational data between October 2011 and October 2012 for a total of 1530 hours on 20 radio-collared individuals. We divided the study period into four biologically relevant seasons: birth and offspring-care with lactation (early wet season from November to January), offspring-care without lactation (late wet season from February to April), mating and early gestation (early dry season from May to July) and late gestation (late wet season from August to October).We followed each radio-collared animal for up to two full nights during each season, with a TR-4 receiver and a RA-14K antenna (Telonics, U.S.A.).The number of focal animal follows per season decreased throughout the year owing to the disappearance of individuals, so that the total number of focal animal follows per individual ranged between 5 and 8 nights (mean ± SD: 7.7±0.8 nights per individual). We restricted our analyses of static and dynamic spatial interactions to adult individuals belonging to seven different social units (Table 1).

Table 1 Summary of continuous focal animal observations conducted throughout the year.

Social Unit	Male ID	hours	N location points	Female ID	hours	N location points
1	**m10**	57	642	**f1B**	87	990
2	**m9**	79	863	**f2**	88	996
3	**m3**	88	946	**f3**	88	964
4	**m4**	90	1008	**f4**	86	991
5	**m5**	88	971	**f5**	88	994
6	**m6**	87	948	**f6**	90	1010
7	**m7**	89	1012	**f7**	87	988

The trees of the spiny forest have small and exposed canopies (Grubb 2003), permitting to observe the animals clearly and continuously, despite their nocturnal activity (Hladik and Charles-Dominique 1974). Continuous focal animal observations (Altmann 1974) started when an animal left its sleeping site at dusk and were continued until it returned to its daytime resting tree at dawn. On average the study animals were out of sight for 7.1±1.8% (mean ± SD) of total observation time. We identified animals ranging in the same area before the onset of data collection during preliminary observations on sleeping site choice and ranging behavior of radio-collared individuals. Henceforth, a second trained observer followed the range-mate of a focal animal simultaneously. We tagged spatial locations of animals during continuous focal observations with biodegradable tape. After each full-night follow, we determined the exact position of the tagged trees with reference to a 10x10m study grid system. Each morning after a full-night follow we located the sleeping trees of all radio-collared animals by radio-tracking to determine the composition of sleeping associations.

We defined social interactions as agonistic, affiliative or neutral. We defined all interactions that were either aggressive (chase, charge, bite and grab) or submissive (flee, be displaced or jump away) as agonistic (*sensu* Pereira and Kappeler 1997). We noted interactions during which animals sat within 1m of each other and/or groomed each other as affiliative. We termed interactions during which animals came within a distance of 5m of each other without exhibiting agonistic or affiliative behavior as neutral. We based calculations of the frequency of social interactions on the time the focal animals were actually in sight.

Data analyses To evaluate static spatial interactions between animals, we calculated individual annual home ranges with the Animal Movement extension of ArcView. We sub-sampled locational data at 5-min intervals for home range analyses. We calculated home range size from 95% fixed kernel home range utilization distributions (Worton 1989) using *ad hoc* smoothing (Silverman 1986). We did not correct for spatial autocorrelation, as kernel densities do not require serial independence of observations when estimating home ranges size, and the accuracy and precision of home range estimates improve with the number of observations (De Solla et al. 1999). We calculated home range overlap in R (R Core Team 2012) using the package ‘adehabitatHR’ (Calenge 2006). To determine whether social units were maintained throughout the year, we calculated overlap of night ranges of simultaneously followed males and females as percent overlap (Kernohan et al. 2001). We calculated overlap of annual home ranges for both, pair partners and same-sexed neighbors. We calculated seasonal influence on night range overlap for pair partners that were followed simultaneously, using one-way repeated-measures ANOVA. We excluded one pair (m10fB1) from the analyses because simultaneous follows on the pair partners were conducted only during the wet season. We averaged values for each season and pair. The data were normally distributed for each level of the within-subject factor season. We conducted the analyses in R using the function ezANOVA in the package ‘ez’ (Lawrence 2012).

We examined dynamic spatial interaction to quantify the degree of sociality between pair partners, i.e. whether they associated, avoided each other or moved randomly in relation to each other. We used three different models: the random gas model (Waser 1976), Hutchinson’s model (Hutchinson and Waser 2007) and Doncaster’s model (Doncaster 1990). We calculated expected rates of encounters between pair partners with the random gas model as $f = \frac{(4 \times \rho \times \upsilon)}{\pi} \times (2d + s)$, where ρ is the density of a species, υ the velocity of an animal, s the group spread and d the distance criterion. We calculated expected rates of associations between pair partners with Hutchinson’s model as $f = n \times \rho \times \pi \times d^2$, where n is the number of instantaneous observations, ρ is the density of a species, and d the distance criterion. For both models, we compared observed rates with expected rates, using Wilcoxon signed-ranks test across all pairs. Using Doncaster’s model, we compared n observed inter-individual distances with expected ones calculated from all n^2 distances possible within a given set of spatial points. We compared observed with expected values for each pair within a 2×2 contingency table containing counts below and above d using a chi-squared test. The significance test depends on successive data points being independent, giving each animal the opportunity to travel to any other part of its range between successive instantaneous observations (Doncaster 1990). We considered data points to be independent as the interval permits an individual to traverse its home range at maximum travel speed (Rooney et al. 1998). Here, we calculated ρ as the inverse of a pair’s union home range in square meters and υ as the average distance the male and female covered during the observation period in meters. We set s to zero and d to 15m as this distance was close enough to allow visual contact between animals.

We used the software R for statistical analyses. We considered alpha levels of $P \leq 0.05$ as statistically significant.

Results

Static and dynamic spatial interactions Average annual home ranges were significantly larger for males (mean ± SD: 0.33±0.08 ha, N = 7) than females (0.18±0.08 ha, N = 7; Wilcoxon rank sum test: W = 47, N = 14, P = 0.005; Fig. 1). Male annual home ranges overlapped on average with those of neighboring males by only 1.65±1.99% and those of females with those of neighboring females by merely 0.4±0.64% (mean ± SD) based on 9 dyads of possible neighbor pairings. However, annual home ranges of particular males and females overlapped considerably. Average overlap between the annual home ranges of the seven pairs identified was 81±20% for females and 43±16% (mean ± SD) for males. Differences between male and female's perspective are due to the smaller home ranges of females.

Average overlap of night ranges was 73±28% for females and 45±24% (mean ± SD) for males based on 6 identified pairs. In general, overlap between pair partners was high throughout all seasons. The maximum observed night range overlap was 100% from the female's perspective and 93% from the male's perspective. Only during 2 out of 48 simultaneous follows did night ranges of pair partners not overlap. Otherwise, minimum observed night range overlap was 26% from the female's perspective and 12% from the male's perspective. Furthermore, season did not have a significant effect on night range overlap from the female's perspective (one-way repeated-measures ANOVA: $F_{3,5} = 1.25$, $P = 0.33$). However, season had an influence on night range overlap from the male's perspective (one-way repeated-measures ANOVA: $F_{3,5} = 3.26$, $P = 0.05$). Night range overlap of males with their corresponding female pair partners was significantly higher during the early dry season (corresponding to mating and early gestation) compared to the late dry season (corresponding to late gestation; Tukey's post hoc test: Z = -3.30, P = 0.005).

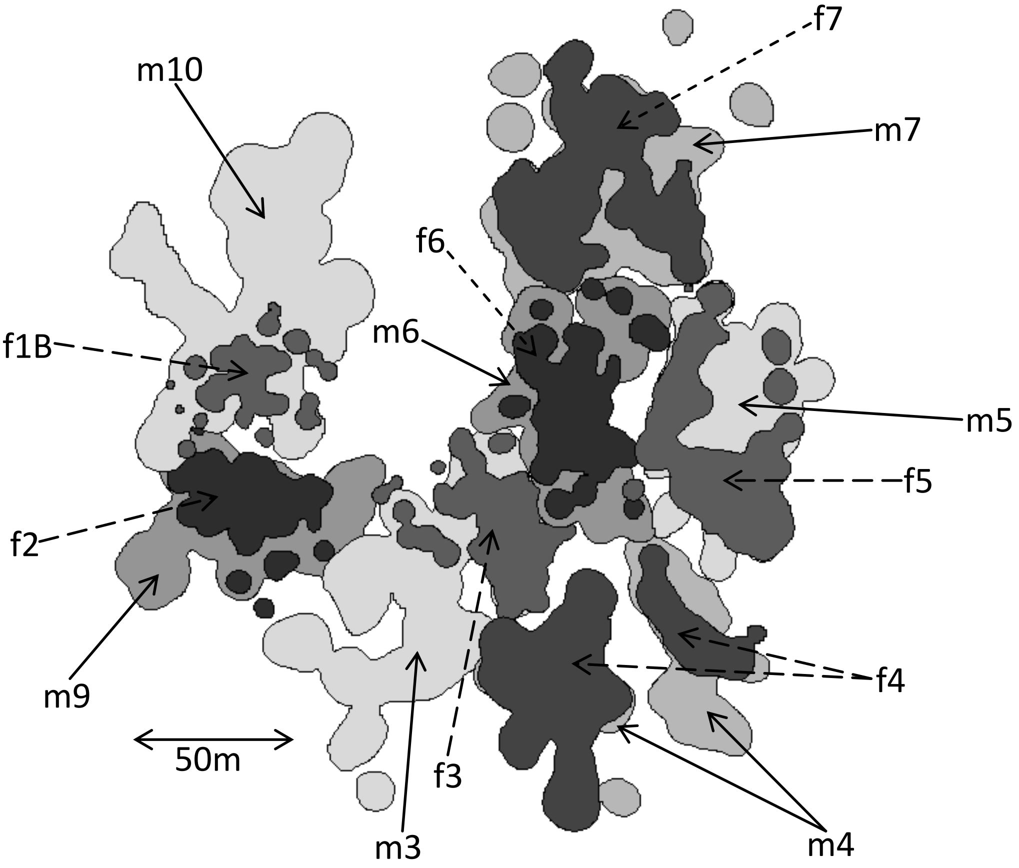

Fig. 1 95% kernel annual home ranges for individual adult males (m) and females (f) of *Lepilemur leucopus* at Berenty between October 2011 and October 2012.

Static spatial interactions between adult individuals changed during the course of the study due to confirmed deaths and dispersal events (Fig. 2). Demographic changes took place within social unit 1, 2 and 7. The home range of male m3 overlapped with those of two females from the beginning of the study, whereas male m10 ranged with two females from March 2012 onwards.

Based on the random gas model, observed encounter rates between pair partners were significantly higher than expected (Wilcoxon signed rank test: V = 28, N = 7, P = 0.02). In contrast, using Hutchinson's model, the number of observed associations was significantly lower than expected (Wilcoxon signed rank test: V = 0, N = 7, P = 0.02). Similarly, observed values were significantly smaller than expected for 5 out of 7 pairs (Chi-squared test: $\chi^2 \geq 3.87$, df = 1, $P \leq 0.049$) and non-significant for the remaining two pairs ($\chi^2 \leq 0.7$, df = 1, $P \geq 0.28$) using Doncaster's model.

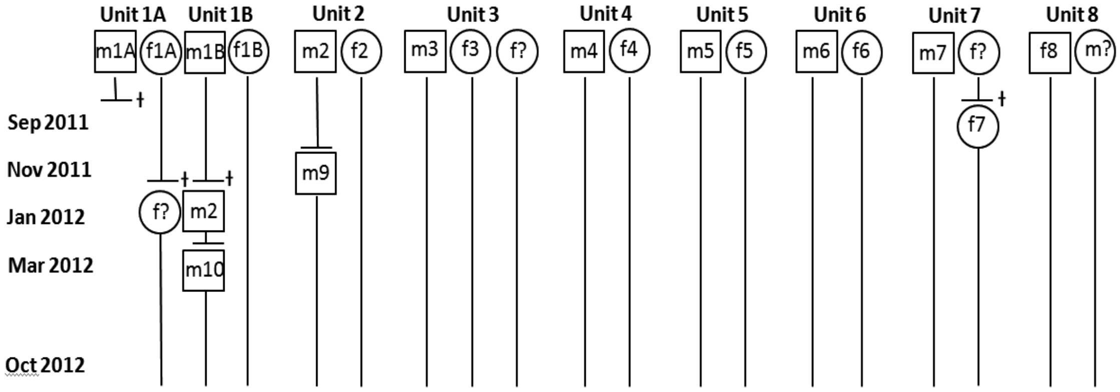

Fig. 2 Demographic changes in the study population between September 2011 and October 2012. Only adult animals are presented. Males are represented by squares; females by circles. Confirmed deaths are illustrated with a cross. No ranging data are available for individuals labeled with a question mark as they were not equipped with radio-collars or died before they could be followed.

Sleeping Associations The study animals spent the day mainly in the confluence of branches of trees of the genus *Alluaudia*, or more rarely inside liana tangles or tree holes. A single adult used 5 to 11 different sleeping sites (Table 2). Although adult individuals shared some of their sleeping trees with their pair partner, they never used them simultaneously (37-69 observation days per dyad). In contrast, adult females and their offspring shared sleeping trees during 79% of 42 observation days, based on six adult females that gave birth in November 2011. However, we never saw adult males sharing a sleeping tree simultaneously with any other member of their social unit. Sleeping trees were never shared with neighbors, neither simultaneously nor consecutively.

Table 2 Number of sleeping trees used exclusively, shared with pair partner and days of simultaneous use.

Pair	Observation days	Exclusive use m/f	Shared use	Days simultaneous use
m10f1B	37	3/3	3	0
m9f2	61	8/4	1	0
m3f3	69	9/3	2	0
m4f4	69	8/4	2	0
m5f5	69	5/4	1	0
m6f6	69	1/2	3	0
m7f7	69	7/2	3	0

Social interactions In total, we observed 72 social interactions during 516 hours of simultaneous focal observations on range mates. The frequency of observed social interactions was therefore low, with only 0.14 interactions/hour across all pairs (Table 3). Most social interactions were of the neutral type (78%), i.e. individuals sitting 1-5m of each other. Agonistic interactions were less common than neutral interactions (21%), whereas affiliative interactions were essentially absent (1%). We never observed allogrooming between adult males and females or social interactions between neighboring males. We only observed a single affiliative social interaction between neighboring adult females (f1B and f2). We did not observe any social interactions between the females of the two social units (1 and 3) with two adult females. However, we observed agonistic interactions between resident and floating males. We did not witness any matings.

Table 3 Frequency and types of social interactions between pair partners. Total number of observation hours: 516.

Pair	Neutral	Agonistic	Affiliative	Total
m10f1B	0.12	0.02	0.00	0.15
m9f2	0.24	0.03	0.01	0.28
m3f3	0.09	0.04	0.00	0.13
m4f4	0.07	0.02	0.00	0.10
m5f5	0.05	0.00	0.00	0.05
m6f6	0.12	0.05	0.00	0.17
m7f7	0.07	0.05	0.00	0.12
Mean	0.11±0.06	0.03±0.02	0.00±0.01	0.14±0.07

Discussion

Static spatial interactions Adult white-footed sportive lemurs had almost exclusive home ranges, as range overlap among neighboring adult males (1.7%) as well as among neighboring adult females (0.4%) was minimal. However, the ranges of certain adult males and females overlapped considerably. Direct social interactions were essentially limited to individuals that shared home ranges. Therefore, spatial boundaries coincided with social boundaries (*sensu* Schülke and Kappeler 2003), and pairs of adult males and females can be regarded as the prevailing social unit of *L. leucopus*.

Currently 24 species of the genus *Lepilemur* are recognized (Ramaromilanto et al. 2009) but only a few have been studied in any detail so far. Two of them, *L. ruficaudatus* and *L. edwardsi,* have been described as pair-living based on spatiotemporal overlap of individual home ranges (Zinner et al. 2003; Méndez-Cárdenas and Zimmermann 2009). Mean overlap of 95% KHRs between pair partners was 61% from the male's and 89% from the female's perspective, whereas mean overlap between neighboring males was 2.3% and 1.8% between neighboring females in *L. ruficaudatus* (Hilgartner et al. 2012). In *L. edwardsi,* mean overlap of minimum convex polygons (MCPs) between pair partners was 72% from the male's and 87% from the female's perspective (Méndez-

Cárdenas and Zimmermann 2009), whereas median overlap between neighboring males was up to 4.9% and up to 6.6% between neighboring females (Rasoloharijaona et al. 2006). Thus, all three *Lepilemur* species studied in detail so far exhibit a pair-living social organization.

Other nocturnal primates vary greatly in patterns of male and female spatial distribution. Home ranges of males show mutual overlap and also overlap with the ranges of several females, whereas female home ranges never do so in the aye-aye (*Daubentonia madagascariensis*; Sterling and Richard 1995). In contrast, home ranges overlap within and between the sexes in mouse lemurs (*Microcebus* spp.; Radespiel 2000; Eberle and Kappeler 2002; Dammhahn and Kappeler 2009), hairy-eared dwarf lemurs (*Allocebus trichotis*; Biebouw 2009), giant mouse lemurs (*Mirza coquereli*; Kappeler 1997), greater galagos (*Otolemur garnettii*; Nash and Harcourt 1986) and slender lorises (*Loris lydekkerianus*; Nekaris 2003). In addition, pair-living has been described for several other nocturnal primate taxa, including fork-marked lemurs (*Phaner pallescens*; Schülke and Kappeler 2003), dwarf lemurs (*Cheirogaleus medius*; Fietz 1999), dwarf galagos (*Galagoides zanzibaricus*; Nash and Harcourt 1986), pottos (*Perodicticus potto*; Pimley et al. 2005), slow lorises (*Nycticebus coucang*; Wiens and Zitzmann 2003), some tarsiers (*Tarsius* spp.; Driller *et al*. 2009; Gursky-Doyen 2010), woolly lemurs (*Avahi* spp.; Harcourt 1991; Norscia and Borgognini-Tarli 2008) and owl monkeys (*Aotus* spp.; Fernandez-Duque 2007). Thus, in terms of ranging patterns, *L. leucopus* do not differ fundamentally from other nocturnal primates.

Sex-specific ranging behavior The fact that males ranged over substantially larger areas than females (95% Kernel: 0.33 ha vs. 0.18 ha) suggests polygynous tendencies of males. According to Schubert et al. (2009a), large home ranges allow males to assess the reproductive status of neighboring females and to monitor the presence of neighboring males. Therefore, male *L. leucopus* may follow a mixed reproductive strategy of maintaining a pair bond while seeking extra-pair copulations, but paternity tests will be required to test this hypothesis because we did not observe any matings. Male home ranges are also larger than female home ranges in *Phaner pallescens* and *Tupaia tana*, which have high rates of extra-pair paternity (Schülke et al. 2004; Munshi-South 2007). Extra-pair copulations were also detected in *L. ruficaudatus*, where males also have significantly larger ranges (95% Kernel: 0.99ha vs. 0.66 ha; Hilgartner et al. 2012). Home range size did not differ between the sexes in *L. edwardsi* (MCP: 2.13 ha for males and 2.07 ha for females; Méndez-Cárdenas and Zimmermann 2009). However, estimates of home range size based on MCPs encompass areas that animals may have never used and therefore may not accurately reflect patterns of range use (Schülke and Kappeler 2003).

While the majority (70%) of social units consisted of pairs, some male *L. leucopus* were associated with two adult females. Similarly, 2 out of 6 males of *L. ruficaudatus* occupied home ranges that overlapped extensively with those of two females (Zinner et al. 2003). However, in *L. ruficaudatus* these two females associated within a shared home range, making it likely that they represented mother-daughter dyads. In contrast, in *L. leucopus* the two females had exclusive ranges as they were regularly seen within the range of the associated adult male but never within the range of the other adult female. Furthermore, all these females were adults because all of them were seen with dependent offspring. In Hladik and Charles-Dominique’s (1974) study of the same population, the largest of four males was associated with five females, while the other males were associated with either one or two females. Based on morphometric data obtained during our capture (unpublished data), the two males that were associated with two females each were not the largest males. However, their home ranges were 40% and 52% larger than the mean home range of the other males, indicating that energetic constraints on territory defense are not a proximate cause for pair-living from the male perspective (van Schaik and Dunbar 1990).

Ecology and ranging behavior Although we studied individuals of *L. leucopus* in a small spiny forest fragment, a crowding effect on ranging patterns seems unlikely. On the one hand, an inverse relationship between density and patch size is frequently observed due to crowding effects of fragmentation (Bowers and Matter 1997). However, estimates of population density of *L. leucopus* at Berenty are much higher for the larger gallery forest (810 individuals per km²) than for the spiny forest (200-350 individuals per km²; Charles-Dominique and Hladik 1971; Hladik and Charles-Dominique 1974). On the other hand, as population densities increase due to crowding effects, average home range size can be expected to become smaller (Cristóbal-Azkarate and Arroyo-Rodríguez 2007) and/or home range overlap between neighboring social units tends to increase (Arroyo-Rodriguez and Mandujano 2006). Although no quantitative data on ranging behavior are available for the gallery forest population, higher population densities in the gallery forest may imply that home ranges of *L. leucopus* are smaller in the gallery than in the spiny forest. In addition, observed home range overlap between neighboring individuals in the spiny forest population was minimal.

Dynamic spatial interactions Using the random gas model, pair partners of *L. leucopus* approached each other more often to within 15m than expected by chance. Schülke and Kappeler (2003) and Hilgartner et al. (2012) also used the random gas model to calculate expected encounter rates in *P. pallescens* and *L. ruficaudatus*, respectively, assuming that it defines the far end of inter-individual spacing within pairs. The results indicated that pair-partners of *P. pallescens* approached each other more often than expected by chance and that encounter rates in *L. ruficaudatus* did not deviate from expected values, which was interpreted as a sign of avoidance. According to the random gas model, spectral tarsiers (*Tarsius spectrum*) living in small family groups were found to spend more time in proximity to other group members than predicted by chance (Gursky 2005).

Hutchinson and Waser (2007) pointed out that the number of expected associations is not given correctly by the random gas model if locational data were collected instantaneously. They proposed a corrected model that is also not affected by variable speed or non-uniform distribution of directions. Using the corrected model, pair partners of *L. leucopus* approached each other less often to within 15m than expected by chance, indicating active avoidance.

Similar results were obtained using Doncaster's model (Doncaster 1990), which allows testing for differences between pairs. Using this model, 5 out of 7 pair partners of *L. leucopus* approached each other less often than expected. The individuals of the two remaining pairs moved randomly in relation to each other. These two pairs had the smallest joint home range areas. Thus, the restricted area available to them may not have allowed them to avoid each other to the same extent as the partners of the other pairs.

The results obtained using the three different models for testing cohesiveness between pair partners varied considerably. To make a more direct comparison of cohesiveness among nocturnal, pair-living primates, we compared the actual percentage of time pair partners spend within 10 m and 20 m of one another during their active period (Table 4). While *Aotus* spp. are among the most cohesive nocturnal pair-living primates, association rates are comparatively low for *Phaner* spp. and *Lepilemur* spp.

Table 4 Overview of percentage of time males and females of pair living nocturnal primates spent in proximity to each other during their activity period.

Species	≤10m	≤20m	Reference
Aotus spp.	100%	100%	Wright 1994
Tarsius spectrum	28%	40%	Gursky 2005
Periodictus potto	?	30%	Pimley et al. 2005
Avahi meridionalis	?	27%	Norscia and Borgognini-Tarli 2008
Phaner pallescens	9%(≤15m)	23%(≤25m)	Schülke and Kappeler 2003
Lepilemur ruficaudatus	9%	20%	Hilgartner et al. 2012
Lepilemur leucopus	7%	23%	This study

Sleeping associations Pair-partners of *L. leucopus* never used the same sleeping tree simultaneously, although they shared some of their sleeping trees on consecutive days. In addition, we observed females actively displacing males from their chosen sleeping tree early in the morning at the end of their active period. *Lepilemur edwardsi* shared sleeping trees on average every second day (Rasoloharijaona et al. 2003). Similarly, *L. ruficaudatus* shared sleeping trees every third to fourth day (Zinner et al. 2003), but they always occupied different tree holes within the same tree (pers. comm. R. Hilgartner). Our study does not support the observation that males and females of *L. leucopus* sleep together during the day (Russell 1977). However, we observed females sharing their sleeping tree frequently with their offspring.

Other nocturnal primates also exhibit much variation in the composition and stability of sleeping associations. Mouse lemurs (*Microcebus* spp.*;* Radespiel et al. 2003; Weidt et al. 2004; Génin 2010), hairy-eared dwarf lemurs (*Allocebus trichotis*; Biebouw 2009) and slender lorises (*Loris lydekkerianus*; Nekaris 2003) sleep in groups of variable size and composition during the day, whereas in aye-ayes (*Daubentonia madagascariensis*; Sterling and Richard 1995) and giant mouse lemurs (*Mirza coquereli;* Kappeler 1997) adults sleep alone. Among pair-living nocturnal primates fork-marked lemurs (*Phaner pallescens;* Schülke and Kappeler 2003), dwarf lemurs (*Cheirogaleus* *medius*; Fietz 1999), dwarf galagos (*Galagoides zanzibaricus*; Nash and Harcourt 1986), tarsiers (*Tarsius spp*.; Driller et al. 2009; Gursky-Doyen 2010), woolly lemurs (*Avahi spp.;* Harcourt 1991,) and owl monkeys (*Aotus spp*.; Fernandez-Duque 2007) regularly sleep together, whereas pottos (*Perodicticus potto;* Pimley *et al*. 2005) and slow lorises (*Nycticebus coucang;* Wiens and Zitzmann 2003) rarely do so. In conclusion, considerable variation exists within nocturnal primates with regard to cohesiveness, as measured by the frequency of sleeping associations, and *L. leucopus* appears to be among the least cohesive species.

Social interactions Although males and females were found to associate in pairs, their rate of social interactions was very low (0.14 interactions/h) and most of their interactions consisted of “sitting within 1-5m”. Similar low interaction rates were described for *L. ruficaudatus* (0.27 per hour; Hilgartner *et al*. 2012) and *N. coucang*, where social interactions made up only 3% of the activity period (Wiens and Zietzmann 2003). However, rates of agonistic interactions were more than 10 times lower in *L. leucopus* than in *P. pallescens* with 0.03 compared to 0.48 interactions per hour, perhaps reflecting the fact that they compete over qualitatively different nutritional resources, i.e. leaves vs. tree exudates (Schülke and Kappeler 2003). Further, while affiliative interactions were exchanged with a rate of 0.22 interactions/h in *P. pallescens*, they were virtually absent in *L. leucopus*. Similarly, affiliative interactions between pair partners were also only very rarely observed in *L. ruficaudatus* (Hilgartner et al. 2012). In contrast, *P. potto* pair-partners engaged in affiliative behavior during 30% of observations and they exhibited no agonistic interactions (Pimley *et al*. 2005). Rates of aggression were also much lower than the rates of affiliation in cohesive pair-living *A. occidentalis* (Ramanankirahina et al. 2011).

Rates of direct social interactions are also low in solitary nocturnal primates. For example, in *M. coquereli*, affiliative interactions were generally rare and in particular between the sexes, whereas agonistic interactions occurred disproportionately often between the sexes (Kappeler 1997). In *M. murinus,* of the 0.12 social interactions/h more agonistic interactions occurred between non-sleeping group members and more affiliative ones between sleeping group members (Dammhahn and Kappeler 2009). Thus, solitary nocturnal primates and those living in dispersed pairs exhibit similarly low rates of social interactions, with *L. leucopus* being at the low end of observed values.

Low rates of social interactions do not necessarily indicate a lack of interaction between individuals. Instead, individuals may regulate their relationships mainly through vocal and olfactory signals (Charles-Dominique 1977). In this context, nocturnal primates use loud calls for sexual advertisement (Zimmermann and Lerch 1993) as well as for group aggregation and coordination (Braune *et al*. 2005). *Lepilemur edwardsi* also uses duets to regulate space use and cohesiveness (Rasoloharijaona et al. 2006), whereas adult *L. ruficaudatus* rarely coordinate vocal interactions and loud calling basically serves to signal an animal's presence in its territory and to regulate spacing among conspecifics (Fichtel and Hilgartner 2012). *Lepilemur leucopus* produced 5 types of loud calls, whose functions need to be studied with future playback-experiments. Olfactory sensitivity and acuity is higher for species living in dispersed pairs, compared to those living in cohesive pairs or groups (Barton 2006). Scent-marking behavior is less well developed in *Lepilemur* than in other lemurs because they do not have scent glands with the exception of paired glands behind the scrotum in males (Petter et al. 1977; Schilling 1979). *L. mustelinus* uses non-nutritive tree gouging as a marking behavior in order to display ownership of sleeping sites while the same behavior is absent in *L. edwardsi* (Rasoloharijaona et al. 2010). Marking behavior in *L. leucopus* is inconspicuous, however, we occasionally observed males placing scent-marks by rubbing their anogenital region against tree trunks, and only males performed branch-bashing displays. Thus, also in terms of communicative complexity, *L. leucopus* ranges near the low end of among primates (McComb and Semple 2005).

Possible causes of pair-living Given the virtual absence of direct male-female association and interaction, it is intriguing to speculate about the possible causes of pair-living in this and other species living in dispersed pairs (Schülke 2005). Sportive lemurs are seasonal breeders with a short mating season around May/June (Randrianambinina et al. 2007; Hilgartner et al. 2008). The short annual mating season and female spatial distribution seem to limit the potential of males to monopolize more than one female in *L. ruficaudatus* (Hilgartner et al. 2012), and in mammals more generally (Lukas and Clutton-Brock 2013). Thus, mate guarding and female defense may be important components of male reproductive strategies. This is reflected by increased night range overlap between pair partners during the mating season (see also Hilgartner et al. 2008). The small female ranges may facilitate monopolization of the ranges of two females for some males. However, *L. leucopus* males and females occupied mutually overlapping home ranges also outside the short annual mating season. Searching for a new mate every year may be more costly than defending the joint territory year-round because of the energetic costs of roaming, increased predation risk during roaming, and the risk of injuries from intrasexual competition (Ralls et al. 2007). Females may potentially profit from year-round associations with a male by territorial defense, and hence reduced food competition (Wrangham 1979), by protection against infanticide (van Schaik and Kappeler 1997) and by paternal care (van Schaik and van Hooff 1983). However, competition for food is low, even during the lean season, indicating that a possible resource defense strategy by males may play only a minor role in this species (unpublished data). While paternal care is absent in sportive lemurs (Hilgartner et al. 2008), infanticide was observed in *L. edwardsi* (Rasoloharijaona et al. 2000) and we observed one case of male infanticide, indicating that infanticide risk may play a role in the evolution and maintenance of dispersed pairs (Opie et al. 2013). Furthermore, females may preferentially mate with males they are familiar with (Fisher et al. 2003), and the stability of pair-bonds may have an effect on long-term reproductive success. In owl monkeys (*A. azari*) stable pairs reproduced once a year, whereas only about 20% of newly formed pairs produced offspring within the first year of pair-formation (Fernandez-Duque and Huck 2013).

Social complexity Using all currently recognized dimensions of social complexity (Freeberg et al. 2012), white-footed sportive lemurs lie at or near the low end of all respective measures. Their modal group size is at the theoretical minimum and they rarely interact with neighbors, i.e. they do not interact frequently with many different individuals. Moreover, observed social interactions with physical contact were limited to bouts of agonism, and neither a single bout of grooming nor mating were observed in > 1500h of observations. In fact, most pair partners actively avoided each other, and most interactions were only recorded because we defined sitting in proximity as a social interaction. Thus, social interactions did also not occur in many different contexts and they occurred with negligible frequencies. Finally, this lack of social complexity was not compensated by high levels of communicative complexity because both the size of their vocal and olfactory repertoire were among the smallest ones reported for primates so far. Thus, we propose that this species of sportive lemur can be used to define a baseline of primate social complexity against which comparable data from other species can be scaled, so that the adjective “highly social” that is increasingly being used to characterize species (e.g. Hoelzl et al. 2007, Bateman et al. 2012) can actually be used in a meaningful way.

Conclusions

White-footed sportive lemurs were found to live in dispersed pairs, resolving questions about their social organization based on earlier studies at the same site. Males and females sharing a home range were characterized by low spatial cohesiveness, including signs of active avoidance, as well as very low rates of direct social interactions. This social system may ultimately be the result of male reproductive strategies, but the determination of the possible causes of pair-living in this species requires further study. In any event, *L. leucopus* is the most asocial of all primates living in pairs studied to date, placing it at or near the primate baseline of social complexity.

CHAPTER 2

Competition for food in a solitarily foraging folivorous primate (*Lepilemur leucopus*)?

With Peter M. Kappeler

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Abstract

Group-living folivorous primates can experience competition for food, and feeding competition has also been documented for solitarily foraging gummivorous and omnivorous primates. However, little is known about the types and consequences of feeding competition in solitary folivorous foragers. We conducted this study in the spiny forest of Berenty Reserve, southern Madagascar, to characterize the competitive regime of the nocturnal solitarily foraging white-footed sportive lemur (*Lepilemur leucopus*), a species that lives in dispersed pairs. We analyzed 1213 h of behavioral observations recorded simultaneously for the male and female of each of 7 social units and recorded seasonal changes in food availability over a complete annual cycle. *Lepilemur leucopus* exhibited low selectivity in its dietary choice and mainly included the most abundant plant species in its diet. Contrary to our predictions, we did not find evidence for increased rates of contest (i.e. displacement from food trees) or scramble competition (i.e. shared use of food patches) during the lean season, neither within nor between social units. Instead, conflict rates were low throughout the year, and, during these observations, any feeding stress may have been more related to food quality than quantity. The resource defense hypotheses may not explain pair-living in this species as there was no indication that males defend food resources for their female pair-partners. The observed lack of feeding competition may indicate that a cryptic anti-predator strategy is a better predictor of spatial avoidance of pair-partners than conflict over food. While anti-predator benefits of crypsis may explain, at least partly, female-female avoidance, studies on the relationship between territory size/quality and reproductive success are required to understand whether feeding competition reduces the potential for female association in *L. leucopus*.

Introduction

Folivorous primates have traditionally been assumed to experience little to no feeding competition as leaves are apparently an abundant and evenly dispersed food resource (Isbell 1991). However, recent studies indicated that at least some folivores experience food limitation (Borries et al. 2008; Harris et al. 2010; Koenig et al. 1998). By exploiting high-quality, patchily distributed, temporally variable food resources, they may experience within-group scramble competition (Snaith and Chapman 2005) as well as within- and between-group contest competition (Koenig 2002). Studies that take place when preferred foods are abundant may not find evidence for food limitation and feeding competition, whereas longitudinal studies on effects of reductions in main food resources may provide valuable insights into the selective pressures that diet places on folivorous primates (Harris et al. 2010).

Previous studies of Malagasy primates (Lemuriformes) revealed that feeding competition does not occur only in group-living species, but also among solitary foragers. For example, within-group scramble and contest competition as well as female feeding dominance were demonstrated for gummivorous *Phaner pallescens* (Schülke 2003). Similarly, resource distribution and resulting competitive regimes have been shown to determine distribution and association patterns of solitary omnivorous *Microcebus berthae* and *M. murinus* (Dammhahn and Kappeler 2009). Competition for food in solitarily foraging folivorous primates has not been studied in detail yet, however.

Sportive lemurs (genus *Lepilemur*) are strictly folivorous and nocturnal. As with other congeners, white-footed sportive lemurs (*Lepilemur leucopus)* have evolved adaptations to a folivorous diet despite small body size (< 1kg), including prolonged resting bouts, small night ranges, an enlarged cecum and cecotrophy (Hladik and Charles-Dominique, 1974). Known predators of sportive lemurs are fossas (*Cryptoprocta ferox*), long-eared owls (*Asio madagascariensis*), Madagascar boas (*Acrantophis sp.*) and Harrier hawks (*Polyboroides radiatus*; Goodman et al. 1993; Rasoloarison et al. 1995; Sussman 1999; Schülke and Ostner 2001; Fichtel 2007). Sportive lemurs live in dispersed pairs, which are characterized by spatial overlap between one adult male and female but low cohesion between pair partners (Schülke and Kappeler 2003; Zinner et al. 2003; Méndez-Cárdenas and Zimmermann 2009; Hilgartner et al. 2012; Dröscher and Kappeler 2013). In *L. leucopus*, pair-partners show signs of active avoidance, and home range overlap among neighboring females is minimal (Dröscher and Kappeler 2013).

If males defend resources that are important to females, instead of defending females directly, resource defense can explain the evolution of pair-living (Emlen and Oring 1977; van Schaik and Dunbar 1990; Wrangham 1979). Under this scenario, female reproductive success is limited by male resource holding potential (Parker 1974), whereas male reproductive success is limited by female choice of mates with variable resource access (Balmford et al. 1992). Pairs evolve under this scenario whenever males are unable to defend territories that can support more than one female (Hilgartner et al. 2012; Lukas and Clutton-Brock 2013). However, to evaluate this hypothesis, quantitative data on resource use and competition are required.

Competition for food may explain female-female avoidance (Lukas and Clutton-Brock 2013) as well as avoidance of pair-partners. For example, pair partners in *P. pallescens* reduce feeding competition by avoiding competitors in time instead of space, as they rely on relatively rare gum trees (Schülke 2003). However, solitary foraging seems to characterize almost all nocturnal primates irrespective of their diet, suggesting that factors other than feeding competition may promote this type of social organization (Schülke 2003). More studies on ranging behavior, resource use and competitive regimes are therefore indicated to further our understanding of the factors that promote intra- and intersexual avoidance in solitary foragers.

The main aims of the present study were to investigate the types and consequences of feeding competition between and within social units of white-footed sportive lemurs. In particular, we predicted contest competition (i.e. displacement from food trees) as well as scramble competition (i.e. food patches shared by individuals) to increase in intensity during the pronounced lean season characterizing southern Madagascar. Alternatively, based on the fact that *L. leucopus* is folivorous and leaves can be expected to be relatively abundant, feeding stress could be more related to food quality than quantity. In this case we predicted scramble as well as contest competition to be rare. In addition, we explored whether female-female avoidance as well as avoidance between pair partners is a consequence of feeding competition. Our second aim was to evaluate the importance of resource defense as a male mating strategy. In this case we predicted that males of neighboring social units would engage in conflict over resources. In the absence of more precise measures of territory quality, we assume that differences in territory quality are related to territory size.

Methods

Study site We conducted our study at Berenty (S 25.00°, E 46.30°), an approximately 200 km^2 private ecotourism reserve. Hot and wet summers characterize Berenty’s semi-arid climate (November to April), which alternate with cold dry and winters (May to October; Jolly et al. 2006). We observed animals in a spiny forest fragment of about 5 ha (HAH Reserve Forestière parcel 1), which is connected to gallery forest on one side via a transitional forest and a further 40 ha spiny forest fragment on the other side (Norscia and Palagi 2008). We recorded minimum and maximum temperatures on a daily basis as well as the amount of precipitation after each rainfall. Seasonality in temperature and rainfall was pronounced during our study. High daytime temperatures with monthly averages of up to 35°C characterized the wet season, while monthly average nighttime temperatures fell to 15°C during the dry season. While precipitation amounted to 480 mm during the wet season, we recorded only 64 mm (or 12% of the annual rainfall) during the dry season. Between 1984 and 2000 annual rainfall at Berenty ranged between 265 and 894 mm, with an average annual rainfall of about 545 mm (Jolly et al. 2002), which corresponds to the 544 mm recorded during our study.

Animal capture To allow continuous focal observations on known individuals, we captured 20 individuals of *L. leucopus* and equipped them with radio-tracking transmitters. We anesthetized animals with 0.4 ml Ketanest (100 mg/ml) in their day-time resting sites, using a blow pipe and 1 ml air-pressured narcotic syringe projectiles (Telinject, Germany). While anesthetized, we fitted the animals with radio transmitters (TW-3 button-cell tags, Biotrack, UK). The assembled transmitter packs weighed 20g and were fastened around the neck of the animals using a coated brass loop that also functioned as antenna. We kept the animals in animal transport boxes until they were fully recovered and released them at their capture site in the evening. The same individuals later reused sleeping trees where they were captured. We fitted adult as well as subadult individuals with radio-collars. We differentiated adult individuals from subadults by their larger degree of tooth wear and body mass. We did not radio-collar juvenile animals (< 1 year old) because radio-collars exceeded 4% of their body mass. We removed all radio-collars after the end of the study. The research adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of non-human primates and was approved by the Commission Tripartite CAFF (Madagascar).

Behavioral observations Five out of seven social units consisted of pairs, whereas in the remaining cases an adult male was associated with two adult females each (social unit 1 and 3; Appendix A). However, these females had exclusive ranges as they were regularly seen within the range of the associated adult male, but never within the range of the other adult female. No behavioral observations could be conducted on these females because they were not equipped with radio-collars. For more detailed information on the identification of the social units within the study population see Dröscher and Kappeler (2013). For the present study, we considered only focal individuals that were adult and belonged to social units for which both the male and the female were radio-collared (N = 16 individuals). We collected behavioral and locational data between October 2011 and October 2012 for a total of 1530 hours.

We divided the study period into four seasons: early wet (November to January), late wet (February to April), early dry (May to July) and late dry season (August to October). We followed each radio-collared animal for up to two full nights during each season with the help of a TR-4 receiver and a RA-14K antenna (Telonics, USA). We started continuous focal animal observations when an animal left its sleeping site at dusk and continued them until it returned to its daytime resting tree at dawn. During continuous focal observations, we tagged all trees the focal animal visited with biodegradable tape in a continuous manner to mark the spatial locations of the animal within its home range. After each full-night follow, we determined the position of the tagged tree with reference to a 10x10m study grid system. We used this method instead of GPS tracking to achieve more precise measurements of spatial locations.

During each feeding bout of a focal animal, we recorded species and types of food eaten along with duration of feeding on that particular food item. A feeding bout started when an individual started to introduce food items into its mouth and ended when an animal stopped inserting food items for more than 15 seconds. To measure contest competition, we recorded agonistic interactions over food resources. We defined all interactions that were either aggressive (chase, charge, bite, and grab) or submissive (flee, be displaced, or jump away) as agonistic (*sensu* Pereira and Kappeler 1997). We defined agonistic interactions as displacements from food patches when the displacing animal foraged in the food patch from which it displaced another individual. To measure scramble competition, we investigated the number of food patches that were used by different individuals, either simultaneously or consecutively.

Food availability We collected phenology data between November 2011 and October 2012. We included as many plant species as possible in the phenology transects, as we did not know at the beginning of the study which species would be consumed by the sportive lemurs. Initially, we tagged 430 individual trees, shrubs and lianas belonging to 105 species along three line transects of 250 m each crossing home ranges of all study animals. We tagged between one and 13 individual plants per species according to their abundance in the forest. We monitored trees twice a month, whereas we monitored shrubs and lianas on a monthly basis. For all plants, we recorded the abundance of young, mature and old leaves as well as fruits and flowers by estimating their crown coverage visually, based on what a full tree would look like, using the following scale: 0 (0%), 1 (1-25%), 2 (26–50%), 3 (51–75%), 4 (76–100%).

We collected information on the local tree community using the point-quarter method (Ganzhorn 2003). We selected points (N = 127) every 20 m with reference to the study grid system covering the entire study area. In each quarter, we measured the distance from the point to the nearest tree with a DBH of > 10 cm and recorded the species identity along with the DBH of the respective tree. To infer species abundance of lianas we used the plot method. We counted all trees with a DBH of > 10 cm carrying lianas, whereby a single tree could carry several liana species. We recorded species identity and abundance of lianas within 10 randomly selected plots of 10x10m.

Data Analyses We calculated tree density (individuals/ha) as 10,000 / (mean point-to-tree distance)^2. We calculated the relative density of a tree species (%) as (number of individuals of a species / total number of individuals) * 100. Finally, we calculated the density of a tree species as (relative density of a tree species / 100) * tree density. To characterize seasonal changes in food availability, we multiplied the density of each food species with its average DBH and the corresponding average abundance of food items recorded during bimonthly phenology surveys, yielding our food availability scores.

We restricted our analyses to behavioral observations where pair-partners (i.e. adult male and female individuals that shared a common range) were followed simultaneously during full night observations by ID and a second trained observer (N = 52 simultaneous observation nights; Appendix A). We subsampled locational data at 5-min intervals for analyses of ranging behavior. We computed nightly average distance between individuals of a pair to examine seasonal changes in inter-individual cohesiveness. We used nearest-neighbor analysis as implemented in the Animal Movement extension for ArcView (Hooge and Eichenlaub 1997) to test for spatial randomness of identified food patches within the territories of the seven social units. We defined food patches as single feeding trees in which animals were observed eating. While R values (obtained by nearest-neighbor analyses) of 1 indicate a random distribution, R values of <1 and >1 indicate a tendency towards a clumped or a uniform distribution, respectively. Significant deviations from the null-hypothesis of complete spatial randomness were tested using Z scores based on Randomization Null Hypothesis computation.

We calculated the sizes of home ranges and core areas from fixed kernel range utilization distributions (Worton 1989) using *ad hoc* smoothing (Silverman 1986). We delineated core areas using a time-maximizing function derived from kernel analyses (Vander Wal and Rodgers 2012). To quantify space-use sharing by pairs, we calculated the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005) of nightly core areas of simultaneously followed individuals. The UDOI takes on values of 0 for two ranges that do not overlap and equals 1 if both utility distributions are uniformly distributed and overlap 100% (Fieberg and Kochanny 2005). We delineated core areas and calculated the utilization distribution overlap indices in R (R Core Development Team 2012) using the code provide by Vander Wal and Rodgers (2012) and the package ‘adehabitatHR’ (Calenge 2006), respectively. We did not correct for spatial autocorrelation, as kernel densities do not require serial independence of observations (De Solla et al. 1999). However, we based our home range estimates on a time interval (i.e. 5 min) that is biologically meaningful, as it allows individuals to traverse their home range at maximum speed (Rooney et al. 1998).

We calculated seasonal influence on scramble competition (i.e. food resource sharing), sociality (i.e. average distance between pair partners and rates of agonistic interactions) and space-use sharing (i.e. as calculated by the UDOI of core areas) for seven pairs, using multilevel modeling (MLM) for a one-way repeated measures design (Field et al. 2012). The advantage of this method over traditional ANOVA is its robustness against violations of sphericity. We averaged nightly values for each season and dyad (N = 28 based on four seasons and seven dyads). Similarly, we analyzed seasonal influences on the activity budgets for the same 14 individuals (N = 56 based on four seasons and 14 individuals). We based estimates of activity budgets (resting, feeding, traveling, other) on the time the animals were in sight.

We analyzed the data using the function ‘lme’ of the R package ‘nlme’ (Pinheiro et al., 2013). For each variable of interest (food resource sharing, average distance between pair partners, rates of agonistic interactions, space-use sharing, time spent resting, time spent feeding and time spent traveling), we specified a separate model. We used season as predictor variable and the respective variable of interest as outcome variable. We set social unit or individual, respectively, as a random factor within the variable season. We fitted the models using maximum likelihood. Based on visual inspection of histograms and q-q plots, residuals did not deviate from a normal distribution. To test whether season had an overall effect on our variables of interest, we compared the full model to a model in which the predictor was absent, using a likelihood ratio test. To investigate the influence of seasonality on overall rates of agonistic interactions, we used non-parametric statistics (i.e. Friedman’s ANOVA), as the data were not normally distributed. We carried out statistical analyses using the software R. We considered an alpha level of $P \leq 0.05$ as statistically significant.

Results

Availability and distribution of food resources We could reliably identify food species and food item consumed during a total of 337 h of feeding observations (total feeding time 349 h) of focal animals (1213 total observation hours). The animals ate mainly leaves (mean = 90.1 ± SD 3.01 %, N = 16); however, they also included flowers (mean = 4.4 ± 3.1 SD %), fruits (mean = 0.6 ± 1.0 SD %) and shoots of non-leafy lianas (mean = 2.5 ± 3.3 SD %) in their diet. In total, we identified food items belonging to 32 species of trees and 16 species of lianas. We recorded a total of 69 tree and liana species at the study site and the animals concentrated their feeding effort on the most abundant species, as usage intensity was highest for the most common tree (i.e. *Alluaudia procera*) and liana species (i.e. *Metaporana parvifolia*; Table 1). A total of 63 % of feeding was spent feeding on the top 5 tree and top 5 liana species based on their abundance. Nearest-neighbor analyses of individual food patches of *Alluaudia procera* and *Metaporana parvifolia*, the two main food species of *L. leucopus*, produced R values ranging between 0.58 and 1.91 (N = 14). Although a tendency to clumping occurred in four cases ($R \leq 0.84$, $P \leq 0.05$), the main food resources of *L. leucopus* generally exhibited a random or even spatial distribution.

Table 1 Tree and liana species at the study site ranked according to their density (individuals/ha) and their usage intensity (% feeding time pooled across all observations and individuals). Food tree and liana abundance were evaluated using different methods and are here considered separately. The top ten contributors to the diet of *L. leucopus* are highlighted in bold (T = tree, L = liana).

Scientific name	Vernacular name	Growth form	Density	%
Alluaudia procera	**Fantsiolotra**	**T**	**369**	**29.76**
Commiphora humbertii	Daro siky	T	147	2.00
Alantsilodendron alluaudianum	**Avoha**	**T**	**85**	**7.26**
Gyrocarpus americanus	Sirosiro	T	79	0.23
Commiphora sp. 2	Daro tandroka	T	60	0.65
Commiphora aprevalii	**Daro be**	**T**	**55**	**3.28**
Salvadora angustifolia	**Sasavy**	**T**	**36**	**4.00**
Alluaudia ascendens	Sogno	T	28	0.28
Euphorbia laro	Famata	T	28	0.00
Commiphora orbicularis	Daro mena	T	21	1.53
Margaritaria sp.	Malamamay	T	21	1.31
Euphorbia sp. 1	Famantamboay	T	21	0.00
Grewia sp. 1		T	15	1.81
Maerua filiformis	Solety	T	13	1.59
Grewia grevei	**Tabinala**	**T**	**11**	**3.20**
Rhigozum madagascariensis	Hazontaha	T	9	0.06
Fernandoa madagscariensis	Somontsoy	T	9	0.01
Albizia sp.		T	6	0.94
Tarenna sp.		T	6	0.01
Strychnos decussata	Relefo	T	6	0.00
Bauhinia grandidieri	**Marovambaka**	**T**	**4**	**2.73**
Boscia longifolia	Somangipaky	T	4	0.90
Maerua nuda	Solety	T	4	0.90
Stereospermum nematocarpum	Hiligne	T	4	0.39

Scientific name	Vernacular name	Growth form	Density	%
Androya decaryi	Hazombolala	T	4	0.34
Grewia sp. 2	Tabarike	T	4	0.16
Cedrelopsis grevei	Katrafay	T	4	0.00
Chadsia sp.	Remote	T	4	0.00
Tetrapterocarpon sp.	Vaovy	T	2	0.70
Commiphora sp. 1	Daro fengoka	T	2	0.06
Alluaudia humbertii	Sognombarika	T	2	0.03
Humbertiella decaryi	Hazombatango	T	2	0.01
Adansonia za	Za	T	2	0.00
Alluaudia demosa		T	2	0.00
Ehretia sp.		T	2	0.00
Euphorbia sp. 2	Famata mainty	T	2	0.00
Mundulea sp.		T	2	0.00
Unidentified species 1		T	2	0.00
Canthium sp.		T	<2	0.84
Commiphora simplicifolia	Daro sengatse	T	<2	0.49
Olax sp.		T	<2	0.31
Rothmania sp.	Tainoro	T	<2	0.10
Albizia tulearensis		T	<2	0.01
Metaporana parvifolia		**L**	**680**	**17.14**
Leptadenia sp.		**L**	**470**	**2.83**
Cynanchum sp.	Try	L	470	0.99
Seyrigia gracilis		L	320	0.01
Hippocratea angustipetalata	**Vahipindy**	**L**	**150**	**2.02**
Asparagus sp.		L	120	0.00
Kalanchoe beauverdii		L	80	0.00
Hildebrandtia valo		L	70	0.10
Plectaneia hildebrantii		L	60	1.19
Combretum sp.		L	60	0.00
Paederia sp.	**Tamboro**	**L**	**40**	**8.28**
Diascorea fandra		L	40	0.00
Menabea venenata	Fiofio	L	30	0.06
Folotsia grandiflorum		L	20	0.14
Ipomoea longituba		L	20	0.12
Craterospermum sp.		L	20	0.00
Diascorea nako		L	20	0.00
Unidentified species 2		L	20	0.00
Unidentified species 3		L	20	0.00
Xerosicyos sp		L	10	0.90
Polygala humbertii		L	10	0.08
Cissampelos pareira		L	10	0.06
Adenia elegans		L	10	0.00
Ipomea sp		L	10	0.00
Unidentified species 4		L	<10	0.18
Clerodendrum sp.		L	<10	0.01

We covered most (25 of 32) of the food tree species via the point-quarter method and calculated food availability scores for these 25 species. Food availability varied seasonally (Fig. 1). While leaves contributed most to available food, flowers and fruits played only a minor role. During the early wet season, young leaves dominated, while mature leaves were most abundant during the late wet and early dry season and reached a low during the late dry season. The animals did not switch to a different diet during the lean season. Instead, during each of the four seasons the animals fed predominantly on the leaves of *A. procera*, followed by *M. parvifolia* during the late wet and early dry season or *Alantsilodendron alluaudianum* during the late dry and early wet season, respectively (Table 2). *Metaporana parvifolia* contributed importantly during all four seasons, whereas *A. alluaudianum* was not among the top 5 contributors during the late wet season.

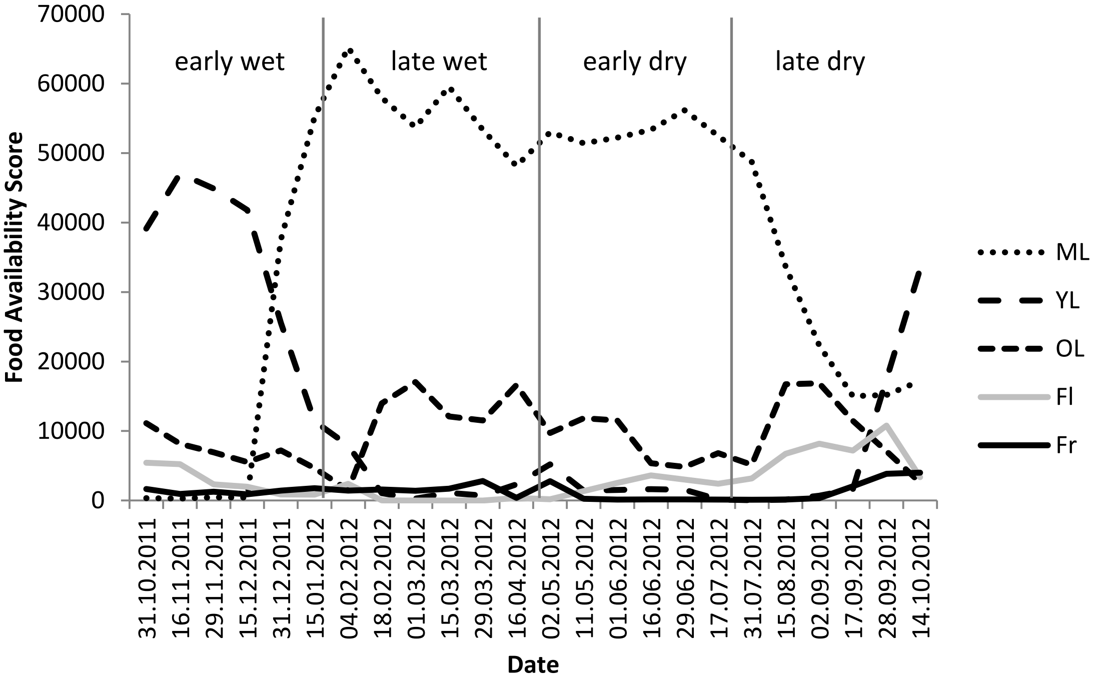

Fig. 1 Seasonal food availability based on 25 identified tree species that were used as a food sources by *L. leucopus* (ML = mature leaves, YL = young leaves, OL = old leaves, Fl = flowers, Fr = fruits).

Table 2 Top five contributors to *L. leucopus* diet according to usage intensity (% feeding time) considered separately for each of the four seasons (L = leaves, Fl = Flowers).

Scientific name	Item	early wet	late wet	early dry	late dry
Alluaudia procera	L	27.9	23.8	34.7	36.3
Metaporana parvifolia	L	7.5	14.4	18.5	6.6
Alantsilodendron alluaudianum	L	12.0		4.2	10.2
Alluaudia procera	Fl				6.9
Paederia sp.	L		8.5	15.7	5.9
Grewia grevei	L		5.0	3.1	
Commiphora humbertii	L		4.7		
Salvadora angustifolia	L	7.3			
Commiphora orbicularis	L	4.3			

Competitive regime We observed displacement from food patches of an adult individual by another adult individual belonging to the same social unit only 3 times during 524.2 h of observation where the focal animal was in sight, resulting in an average rate of 0.006 displacements / h. In all 3 cases, it was a female who displaced a male from the food patch. Furthermore, displacements from food trees were never observed between individuals belonging to different social units. Across all seasons, a pair used on average 37 ± 9 food patches (N = 52 simultaneous observation nights). Of these food patches, an average of only 3 ± 2 (or 8 ± 5 %) were used by both members of a pair during the same night. On only 4 occasions did we see adult individuals foraging simultaneously in the same food patch. We never saw individuals belonging to different social units feeding simultaneously in the same food patch. We identified on average 189 ± 21 (N = 7) food patches within a single territory across all four seasons. Only 32 ± 8 (or 17 ± 5 %) of these were used by both adults of a social unit. Of the total of 1320 food patches only 5 were used by individuals from different social units, in each case neighboring females.

Seasonal influences Season neither had a significant effect on the amount of food patches that were used by both pair-partners (MLM: $\chi^2(3) = 1.36$, $P = 0.71$), nor on their average cohesion (MLM: $\chi^2(3) = 0.49$, $P = 0.92$), nor on space-use sharing (i.e. UDOI) of core areas (MLM: $\chi^2(3) = 0.67$, $P = 0.88$), nor on their average rates of agonism (Friedman's ANOVA: $\chi^2(3) = 5.49$, $P = 0.14$; Table 3). However, season had a significant effect on the amount of time animals spent resting (MLM: $\chi^2(3) = 16.24$, $P = 0.001$), eating ($\chi^2(3) = 12.72$, $P = 0.01$) and travelling ($\chi^2(3) = 20.25$, $P < 0.01$; Fig. 2). Time spent resting was significantly higher during the early dry, compared to the late wet season (Tukey's post hoc test: $Z = 2.967$, $P = 0.02$). In addition, the animals spent significantly less time resting during the late dry compared to the early dry season ($Z = -4.283$, $P < 0.01$). The animals spent significantly more time eating during the late dry, compared to the early wet ($Z = 2.767$, $P = 0.03$) and early dry season ($Z = 3.387$, $P < 0.01$). The animals travelled significantly less during the early dry compared to the early wet ($Z = -5.066$, $P < 0.01$) and late wet season ($Z = -2.906$, $P = 0.02$) as well as significantly less during the late dry compared to the early wet season ($Z = -2.746$, $P = 0.03$).

Table 3 Seasonal values (average ± SD) for the amount of food patches used by both pair-partners, for cohesion measured as average distance between pair-partners, for space-use sharing of core areas by pair-partners based on UDOI, and for the rate of agonistic interactions between pair partners (N = 7).

Season	Food patch sharing (%)	Cohesion (m)	UDOI of core area	Agonistic interactions/h
early wet	8.98 ± 2.28	33.92 ± 10.00	0.12 ± 0.08	0.08 ± 0.08
late wet	7.32 ± 4.42	33.39 ± 5.81	0.10 ± 0.05	0.05 ± 0.05
early dry	8.29 ± 3.97	33.77 ± 4.54	0.12 ± 0.07	0.01 ± 0.02
late dry	7.00 ± 4.17	34.99 ± 8.31	0.10 ± 0.06	0.01 ± 0.02

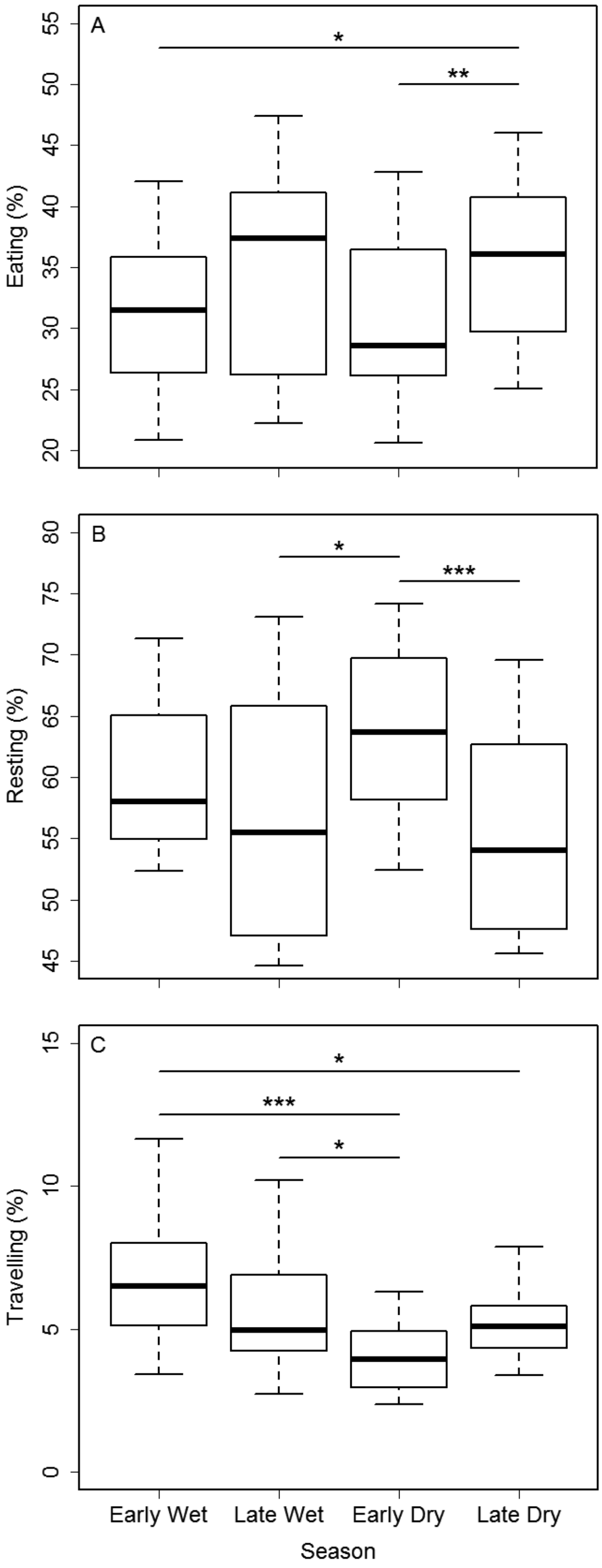

Fig. 2 Boxplots showing medians and quartiles of the proportions of total observation time *Lepilemur leucopus* spent eating (A), resting (B) and travelling (C) across four seasons (N = 14; multilevel modeling (MLM) for repeated measures, *P<0.05, **P<0.01, ***P<0.001).

Predation pressure Between October 2011 and August 2013, we recorded the death or disappearance of 9 of 21 individually known animals. In two cases we found the dead body without signs of external injury. In four cases we could assign the death of the individual to predation. On several occasions we observed introduced African wild cats (*Felis silvestris*) to approach or attack *L. leucopus*. We found the remains (guts, head and tail) of one victim, and characteristic tooth marks on the radio-collars of 3 disappeared individuals. In three additional cases animals disappeared and were never re-sighted. Therefore, during a period of about two years the disappearance of at least 19% and perhaps up to 33% of the study animals could be attributed to predation.

Discussion

Competitive regime Contest feeding competition between neighboring social units of *L. leucopus* is presumably very weak, as we did not observe any displacements from food patches. Similarly, within social units, we observed displacement from food patches only at a negligible rate. When they occurred, it was the female that displaced the male, which may indicate female dominance, which is widespread among other lemurs (Kappeler 1993). Scramble competition between social units of *L. leucopus* was also not pronounced, as a negligible number of food patches was used by individuals of neighboring social units, perhaps because adjacent home ranges overlap only little (Dröscher and Kappeler 2013). Finally, the number of shared food patches within pairs was also low, despite extensive mutual home range overlap.

Solitary foraging *per se* cannot explain the absence of feeding competition in *L. leucopus* as other species of solitary foragers were found to experience feeding competition. The competitive regime of *M. berthae*, for example, is characterized by within-group scramble competition, whereas the competitive regime of *M. murinus* is additionally characterized by between-group contest (Dammhahn and Kappeler 2009). *Microcebus berthae* mainly feeds on the secretion of homopteran larvae, which occur in small dispersed patches that can be depleted by a single individual, whereas *M. murinus* spends a substantial amount of time foraging on gum and fruit trees, which are large, high-quality resources that can be monopolized. In *M. berthae,* females that overlap with many other females have larger home ranges and range further than females that overlap with fewer other females. In *M. murinus* displacement from high-quality resource patches occurs, but aggression is mainly targeted at individuals that are not part of female sleeping associations.

The competitive regime of *P. pallescens* is characterized by strong within-group scramble and contest competition (Schülke 2003). The most important food species is a relatively rare gum-producing tree, and the majority of the trees are used by both pair-partners. Direct contest for food is reflected by a high rate of agonistic inter-sexual interactions. Females displace males from food trees, and avoidance of direct competition is achieved by differential timing of resource use. Physical condition of females is negatively correlated with family size, indicating strong within-group scramble competition. In contrast, *L. leucopus* relied on common tree and liana species, similar to *L. edwardsi* (Thalmann 2001).

Theory suggests that high selectivity for uncommon food items distributed in clumped patches creates the potential for food competition (Grueter et al. 2009), while competition can be expected to be low when the diet is based on abundant and evenly distributed food resources (Terborgh and Janson 1986). Based on these principles, the absence of competition in *L. leucopus* might be explained by their low selectivity in dietary choice, as they primarily used the most abundant plant species.

Seasonality Despite seasonal variation in food availability, with a minimum of food availability during the late dry season, season affected neither the intensity of competition nor the nature of social interactions in *L. leucopus*. This pattern contrasts with that seen in spectral tarsiers (*Tarsius spectrum),* in which a seasonal decrease in food abundance leads to decreased cohesion between family members and increased territorial disputes (Gursky 2000). This finding, together with the overall low rates of competition regardless of season, suggests that feeding competition cannot be regarded as a dominant ecological pressure in *L. leucopus*, at least at this site in years with average, or better, rainfall.

A steep decline in food availability can lead to physiological and behavioral costs in folivorous primates (Harris et al. 2010), and one may expect adaptive strategies such as dietary specialization, ranging and/or physiological adaptations to overcome periods of food scarcity (Hemingway and Bynum 2005). *Lepilemur leucopus* did not switch to a different diet during the late dry season; instead, it fed predominantly on leaves of *A. procera* regardless of season. Similarly, food choice and dietary diversity were similar during the wet to the dry season in *Lepilemur petteri* (Nash 1998). *Lepilemur leucopus* minimized its energy expenditure during the early dry season by resting more and travelling less. This time corresponded to a period when temperatures reached a minimum, but leaves were still abundant. During the late dry season, when temperatures increased again but food availability reached a low, activity returned to pre-dry season levels, indicating that *L. leucopus* might be seasonally more affected by cold stress than by food limitation. Likewise, *L. petteri* conserved energy during the cool dry season by resting more and travelling less (Nash 1998), and *L. ruficaudatus* did not experience energetic constraints due to restricted food supply during the dry season as indicated by their body condition (Ganzhorn 2003). Thus, *L. leucopus* may be more constrained by food quality than abundance. In addition, sportive lemurs are characterized by low resting metabolic rates (Schmid and Ganzhorn 1996). Further studies investigating C-peptide levels, an indicator of energy balance, across different seasons might provide more insights into possible physiological costs of reduced food availability (Harris et al. 2010).

Resource defense as a male strategy While resource-defense is a common mating strategy among birds (Emlen and Oring 1977), males defend resources to attract females in only a few mammalian species (Greenwood 1980). However, males play an important role in resource defense in several primate species (spider monkeys: Aureli et al. 2006; capuchins: Crofoot 2007; guerezas: Fashing 2001; bamboo lemurs: Nievergelt et al. 1998; tamarins: Peres 1989; sakis: Thompson et al. 2012; chimpanzees: Williams et al. 2004). For example, in frugivorous chimpanzees (*Pan troglodytes*), males defend a feeding territory for themselves and the resident females (Williams et al. 2004). In folivorous guerezas (*Colobus guereza*), intensity of intergroup aggression between adult males is related to the frequency of food patch use at intergroup encounter sites (Fashing 2001). In contrast, males of *L. leucopus* did not engage in intergroup aggression related to food resources.

Males are expected to adopt the resource defense strategy when food is limiting and distributed in defensible patches, when females are reproductively monopolizable, and when females choose to mate with males that defend resources (Fashing 2001). Although *Lepilemur* females are reproductively monopolizable, as mate-guarding is intense during the short mating season (Hilgartner et al. 2012), food is not distributed in defensible patches, as indicated by the preferential use of the most abundant plant species with random spatial distribution. Moreover, females of *L. ruficaudatus* were never observed to terminate a pair-bond or to try to repel a new immigrant male (Hilgartner et al. 2012). Likewise, none of our study females was observed to transfer to another social unit. Although long-term data are required to obtain better information on the role of female choice in this species, it seems that *Lepilemur* males cannot achieve greater reproductive success by defending resources for females.

Furthermore, the resource defense hypothesis predicts that an expansion in territory size should lead to an increase in female reproductive rates due to an increase in food availability (Williams at el. 2004). In contrast, the mate defense hypothesis predicts that an expansion in territory size should lead instead to an increase in the number of adult females (Wrangham 1979). The two males in our population that defended the largest territories were associated with two females each (Dröscher and Kappeler 2013). These females had the smallest and the third-smallest home range, respectively, indicating that females do not necessarily benefit from male range expansion in terms of increased food availability. However, we assume that differences in territory quality are related to territory size in this species and further studies incorporating more precise measures of territory quality are required to advance our understanding of the importance of male resource defense as a mating strategy in *L. leucopus*.

Intersexual spatial avoidance Sportive lemurs are characterized by low spatial cohesiveness, including active avoidance of pair partners (Dröscher and Kappeler 2013; Hilgartner et al. 2012). The observed intersexual avoidance cannot be explained by avoidance of competition over food resources, as conflicts over food resources were rarely observed, and inter-individual avoidance did not increase when food availability was low.

Diurnal primates benefit from living in cohesive groups as it provides enhanced protection against predation (Dehn 1990), and groups are larger and more cohesive where individuals are exposed to a high predation risk (Clutton-Brock and Janson 2012). While diurnal social primates rely on early detection and warning of approaching predators, solitariness and crypsis is a viable alternative anti-predator strategy for solitary foragers (Terborgh and Janson 1986). The fossa is a specialist predator of lemurs (Dollar et al. 2007; Karpanty and Wright 2007), and half its prey items are lemurs with a high prevalence of medium-sized nocturnal species (Hawkins and Racey 2008). While fossas are no longer present at the study site, we could confirm the presence of African wild cats, which have been observed to prey upon much larger Verreaux's sifaka (*Propithecus verreauxi*; Brockman et al. 2008).

Predation poses an important ecological pressure for *L. leucopus* as mortality rates due to predation were high. Similarly, predation rate on *L. ruficaudatus* was 36% during a four-year study (Hilgartner et al. 2008). Sportive lemurs produce alarm calls only when predators directly attack them (Fichtel 2007). The lack of an early warning system against predators seems to be a reason why sportive lemurs do not spend more time together (Fichtel et al. 2011). Thus, anti-predator benefits of crypsis may explain intersexual spatial avoidance of pair partners as this strategy decreases conspicuousness. However, *L. leucopus* produces loud calls to communicate with pair-partners and/or neighbors. As *L. leucopus* are highly territorial, a trade-off between the need to signal their presence in their territory (Rasoloharijaona et al. 2006; Fichtel and Hilgartner 2013) and the need to avoid detection by predators seems to exist. Further studies should investigate if and how individuals adjust their loud-calling behavior during times of potentially heightened predation risk such as during the dry season when crown coverage is reduced, or during full moon when ambient light levels are increased.

Intrasexual spatial avoidance The spatio-temporal distribution of females is one of the main aspects underlying variation among mating and social systems (Arnold and Duvall

1994), and spatial dispersion of females appears to be the best predictor of pair-living in mammals (Komers and Brotherton 1997; Lukas and Clutton-Brock 2013). High levels of female intrasexual avoidance are indicated by a virtual absence of home range overlap in *L. leucopus* (Dröscher and Kappeler 2013). According to Koenig et al. (2013), possible determinants of female spatial dispersion are anti-predator benefits of crypsis (Clutton-Brock and Janson 2012), the dependence on non-divisible resources (Schülke and Kappeler 2003) or a low abundance of large resources (Delgado and van Schaik 2000).

While an anti-predator strategy based on crypsis may explain at least partly female spatial avoidance in *L. leucopus*, other factors may be important as well. Female reproductive success is generally limited by access to resources (Emlen and Oring 1977). When food is spatially clumped, females are expected to be more aggregated and less territorial, as food resources are not economically defendable. In contrast, when food is spatially dispersed, it can be expected that interactions among females are decreased and the costs of home range defense are reduced, and that females are more territorial (Maher and Lott 2000; Schubert et al. 2009a). As we included only food patches that were actually visited in our nearest-neighbor analyses, the results presented above are biased against finding random patterns. Nevertheless, in most cases the main food resources showed a random or even distribution. To examine in more detail whether scramble competition for food reduces the potential for female association, future studies on the effects of territory size and quality on female reproductive success of females would be required (Koenig 2002).

Conclusions

Competitive costs of feeding competition were negligible within and between social units of *L. leucopus*, presumably due to low dietary selectivity and reliance on the most common food species. As seasonal food scarcity was not reflected by feeding competition, *L. leucopus* is ecologically more constrained by food quality than quantity. Pair-living in this species is probably not the result of male resource defense. Intersexual avoidance between pair-partners is best explained by anti-predator benefits related to crypsis. The factors favoring female-female avoidances may include crypsis-related anti-predator benefits and feeding competition, but they could not be conclusively identified by the present study.

CHAPTER 3

Maintenance of familiarity and social bonding via communal latrine use in a solitary primate (*Lepilemur leucopus*)

With Peter M. Kappeler

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Abstract

Latrine use (i.e. the repeated use of specific defecation/urination sites) has been described for several mammals, including carnivores, ungulates and primates. However, the functional significance of latrine use in primates has not been studied systematically yet. We therefore followed 14 radio-collared individuals of the pair-living white-footed sportive lemur (*Lepilemur leucopus*) for 1097 hours of continuous focal observations to investigate latrine distribution, seasonality of latrine use as well as age and sex of users to test various hypotheses related to possible functions of latrine use, including territory demarcation, resource defense, signaling of reproductive state, social bonding and mate defense. All individuals of a social unit exhibited communal use of latrines located in the core area of their territory, supporting the social boding hypothesis. Latrine use seems to facilitate familiarity and social bonding within social units via olfactory communication in this primate that lives in family units but exhibits low levels of spatial cohesion and direct social interactions. In addition, frequency of latrine visitation was higher during nights of perceived intruder pressure, supporting the mate defense hypothesis. However, animals did not react to experimentally introduced feces from neighboring or strange social units, indicating that urine may be the more important component of latrines than feces in this arboreal species. Based on a survey of latrine use and function in other mammals, we conclude that latrines facilitate communication particularly in nocturnal species with limited habitat visibility and in species where individuals are not permanently cohesive because they constitute predictable areas for information exchange.

Introduction

Chemical signals can transmit a variety of information in vertebrates, such as species identity (Caspers et al. 2009), sexual identity (Ferkin and Johnston 1995), reproductive state (Ziegler 2013) and individual identity (Linklater et al. 2013). Many chemical signals derive from various excretory products, such as feces, urine and gland secretions (Eisenberg and Kleiman 1972), and scent-marking is defined as the application of these products to features in the environment (Macdonald 1980). The repeated use of specific locations for defecation/urination can result in an accumulation of feces and other excretory products at so-called latrine sites and this behavior can be considered a special form of scent marking in cases where it serves a communicatory function (Wronksi 2013). Latrines have been described for several ungulates (e.g. *Ourebia*: Brashares and Arcese 1999; *Tragelaphus*: Apio et al. 2006; *Mazama*: Black-Decima and Santana 2011; *Gazella*: Wronski et al. 2013), carnivores (e.g. *Suricata*: Jordan et al. 2007; *Vulpes*: Darden et al. 2008; *Meles*: Kilshaw et al. 2009; *Hyaena*: Hulsman et al. 2010), primates (e.g. *Lepilemur*: Charles-Dominique and Hladik 1971; *Cheirogaleus*: Schilling 1980a; *Hapalemur*: Irwin et al. 2004) and a few other mammalian taxa (e.g. *Arvicola*: Woodroffe and Lawton 1990; *Oryctolagus*: Sneddon 1991). Feces are either deposited alone (e.g. *Bassariscus astutus*: Barja and List 2006; *Ourebia ourebi*: Brashares and Arcese 1999) or together with urine and/or secretions of specialized glands at latrine sites (e.g. *Meles meles*: Roper et al. 1986; *Mazama gouazoubira*: Black-Decima and Santana 2011). In several species (e.g. *Vulpes velox*: Darden et al. 2008; *Hyaena* spp.: Gorman and Mills 1984; *Meles meles*: Stewart et al. 2002) urination is the most common mark used in this context, and feces per se may not be the most important information component of a latrine (Darden et al. 2008). Similarly, for arboreal species one could reasonably expect that any potential communicatory function may be rather related to olfactory signals obtainable from arboreally deposited urine than from terrestrial accumulation of feces, which may rather be a byproduct of localized urine marking.

Among primates, the lemurs of Madagascar (Lemuriformes) represent a radiation whose members rely heavily on chemical signals for their social communication (Mertl 1976; Schilling 1979, 1980b; Perret 1992; Kappeler 1998; Heymann 2006b; Charpentier et al. 2008; Boulet et al. 2009; Crawford et al. 2009; Boulet et al. 2010; Charpentier et al 2010; Morelli et al. 2013), irrespective of their social organization (Kappeler and van Schaik 2002). The more than 20 species of sportive lemurs (genus *Lepilemur*) are all medium-sized nocturnal folivores. Like many other nocturnal lemurs, they exhibit urine marking (Schilling 1979, 1980b; Epple 1986). In addition, *Lepilemur* males posses anogenital scent-glands, while females have no scent-glands (Petter et al. 1977; Schilling 1979). Sportive lemurs are strictly arboreal, and patterns of defecation/urination produce terrestrial accumulations of feces (Charles-Dominique and Hladik 1971; Russell 1977; Irwin et al. 2004). Some species live in dispersed pairs, which are characterized by spatial overlap between one adult male and one adult female, but low cohesion between pair partners (Schülke and Kappeler 2003; Zinner et al. 2003; Méndez-Cárdenas and Zimmermann 2009; Hilgartner et al. 2012; Dröscher and Kappeler 2013). Pair-partners living in dispersed pairs may never share sleeping sites or allogroom each other, and they may even show signs of active spatial avoidance (Dröscher and Kappeler 2013). In addition, sportive lemurs are highly territorial, as indicated by minimal home range overlap between individuals of neighboring social units (Zinner et al. 2003; Rasoloharijaona et al. 2006; Méndez-Cárdenas and Zimmermann 2009; Dröscher and Kappeler 2013). This combination of traits makes sportive lemurs an interesting taxon to study various potential functions of latrines.

Irwin et al. (2004) reviewed latrine behavior in primates and discussed several hypotheses for the function of latrine use. In particular, they suggested that latrine use in lemurs is mainly linked to the defense of resources, such as specific food patches, mates or sleeping sites. While male sportive lemurs exhibit mate guarding and defend their territories against neighboring males (Hilgartner et al. 2012), they do not defend food resources for their pair mates, and competition for food is low within as well as between social units (Dröscher and Kappeler 2014). However, systematic tests of this potential function of latrines have not been conducted yet.

While latrines may be merely a by-product of a bimodal defecation rhythm that results in the concentration of defecations being deposited under repeatedly used sleeping sites (Julliot 1996; González-Zamora et al. 2012), the use of localized defecation sites can also be explained by several additional, non-exclusive functional hypotheses. Many hypotheses that are commonly formulated for the function of scent marking (e.g. Ralls 1971; Kappeler 1998; Brady and Armitage 1999; Lazaro-Perea et al. 1999; Rostain et al. 2004; Heymann 2006a; Lewis 2006) are also applicable to the function of latrine use, as latrine behavior is a special form of olfactory communication.

In the following, we present hypotheses that are applicable to the social system of our study species (see below) and provide key references for each one of them. First, latrines may be used to demarcate territories, since many mammals are known to use urine, feces or other scent-marks to delineate home range boundaries (Mertl-Milhollen 1979; Brashares and Arcese 1999; Stewart et al. 2001; “territory demarcation hypothesis”). Second, latrines may be used to communicate reproductive state, since male mammals seem to be able to detect chemical cues in female urine and/or feces related to reproductive state (Balestrieri et al. 2011; Archunan and Rajagopala 2013; “reproductive signaling hypothesis”). Third, latrines may serve to advertise the willingness to defend important resources such as food (Kruuk 1992; Miller et al. 2003; Remonti et al. 2011) or resting sites (Goszczynski 1990; Branch 1993; Brady and Armitage 1999; “resource defense hypothesis”). Fourth, latrines may function as information exchange centers for individuals that rarely associate or interact directly to facilitate the exchange of olfactory individual-specific information within social units to maintain social bonds (Kingdon 1982; Greene and Drea 2014; “social bonding hypothesis”). Finally, latrines may play a role in mate defense by advertising the commitment of resident males to defend resident females (Roper et al. 1986; Jordan et al. 2007; “mate defense hypothesis”).

By detailing latrine density and distribution, seasonality and behavioral contexts of latrine use as well as age and sex of users, we aimed to test predictions of the above hypotheses. Specifically, (1) if latrines were used to demarcate territories, we expected that they would be located at territorial boundaries or in zones of home range overlap between neighboring social units rather than in core home range areas. (2) If latrines were used to communicate reproductive state, we predicted that frequency of latrine use would increase during the pronounced annual mating season. (3) If latrines were used to contribute to resource defense, we anticipated that latrines would be located in proximity to regular sleeping trees, that feeding effort would be higher within than outside the latrine area, and/or that animals would mark specific food trees by defecation/urination. (4) If latrines were used as information exchange centers for intra-group communication in a species in which individuals of a given social unit visit latrines independently, we expected all individuals of a social unit to visit the same latrines to facilitate information transfer. In addition, we predicted that latrines would be visited exclusively by individuals of a social unit, but not by individuals of neighboring units. (5) If latrines play a role in mate defense, we expected that the frequency of male latrine use would increase with perceived intruder pressure. In addition, we expected that males would place glandular scent-marks preferentially in latrines. Finally, (6) since aggression in *L. leucopus* is directed towards roaming individuals rather than neighbors (Dröscher and Kappeler 2013), we expected individuals to react more strongly to experimentally introduced feces of strange individuals than to those of familiar ones (Ydenberg et al. 1988; Müller and Manser 2007).

Methods

Study site and animal capture We studied a population of white-footed sportive lemurs (*Lepilemur leucopus*) at Berenty (S 25.00°, E 46.30°), an approximately 200 km^2 private ecotourism reserve in southern Madagascar. We observed animals in a spiny forest fragment of about 5 ha (HAH Reserve Forestière parcel 1), which is connected to gallery forest on one side via a transitional forest and a further 40 ha spiny forest fragment on the other side (Norscia and Palagi 2008). To ensure continuing focal observations of single individuals, we equipped animals with radio-tracking transmitters. We used a blowpipe and 1 ml air pressured narcotic syringe projectiles (Telinject, Germany) to anesthetize animals with 0.4 ml Ketanest (100 mg/ml) in the mornings in their daytime sleeping sites. We fitted the animals with radio-collars (TW-3 button-cell tags, Biotrack, UK) while anesthetized. We kept the animals in an animal transport box until they were fully recovered and released them again at their capture site in the evening. We fitted 16 adult (eight males and eight females) and four subadult individuals (three males and one female) with radio-collars. We differentiated adult individuals from subadults by the degree of tooth wear and body mass. We did not radio-collar animals when radio-collars exceeded 4% of their body mass. We removed all radio-collars after the end of the study. The research followed standard protocols for animal handling, capture and radio-tracking and was approved by the Commission Tripartite CAFF of the Ministry for Water and Forests (Madagascar).

Behavioral observations We collected behavioral and locational data between October 2011 and October 2012 for a total of 1530 hours on 20 radio-collared individuals. For the present study, we only considered focal individuals that were adult and belonged to social units in which both pair mates were radio-collared (N = 14 individuals, observation time in sight = 1097 hours). Five out of seven social units consisted of pairs, whereas in the remaining cases an adult male was associated with two adult females each (social unit 1 and 3). However, these females had exclusive ranges since they were regularly seen within the range of the associated adult male, but never within the range of the other adult female. No behavioral observations could be conducted on these females because they were not equipped with radio-collars. For a detailed description on the identification of the social units within the study population see Dröscher and Kappeler (2013).

We divided the study period into four biologically relevant seasons: birth and offspring-care with lactation (early wet season from November to January), offspring-care without lactation (late wet season from February to April), mating and early gestation (early dry season from May to July) and late gestation (late dry season from August to October). Each individual was watched for two full nights during each season, once by the first author and once by a Malagasy research assistant, using a TR-4 receiver and a RA-14K antenna (Telonics, U.S.A.; Appendix A) to locate animals. However, we included data only for 7 observation nights for male m9 since he joined female f2 only after he displaced the previous resident male. Similarly, we include data only for 4 observation nights for male m10 since he only joined female f1B at the beginning of the mating season.

The trees of the spiny forest have small and exposed canopies (Grubb 2003), permitting nocturnal observation of the subjects clearly and continuously (Hladik and Charles-Dominique 1974). We started continuous focal animal observations (Altmann 1974) when an animal left its sleeping site at dusk until it returned to its daytime sleeping site at dawn. Usually, when the first author watched an adult male, the Malagasy research assistant watched the corresponding adult female during the same night simultaneously and vice versa. An overview of the focal animal observations is given in Appendix A. We tagged spatial locations of animals during continuous focal observations with biodegradable tape while recording the beginning and end of each behavior (i.e. resting, travelling, grooming, feeding, displaying, social interactions). We determined the exact position of the tagged trees with reference to a 10x10m study grid system. In addition, we recorded all occurrences of defecation, urination, scent marking (i.e. rubbing of the anogenital region on a substrate) and olfactory inspection (i.e. sniffing and licking of substrate) of the focal animals along with their spatial location. We distinguished between single-use and multiple-use defecation sites by investigating the degree of ground coverage by feces (a few scattered droppings that could have been produced by a single defecation event vs. concentrated accumulation of feces indicative of multiple use). In addition, ID recorded the same data every time she could observe an un-collared animal defecating/urinating. Each morning after a full-night follow, we located the sleeping trees of all radio-collared animals.

Experimental translocation of feces To establish whether animals discriminate between feces of their own, neighboring and strange social units, we conducted latrine translocation experiments in June 2013 with males and females of 5 social units. We gathered feces from latrines from known neighboring social units (i.e. “neighbor treatment") and from latrines we located in a neighboring forest parcel, to ensure that the feces originated from social units that were not familiar to the focal animals (i.e. "stranger treatment"). Similarly, we gathered feces from latrines of the focal social unit (i.e. "control treatment"). For the experiments, we spread the gathered feces on plastic sheets of approximately 1m^2 (i.e. "experimental latrine"). We handled the feces using disposable plastic gloves. To ensure that the focal animals would encounter the experimental latrines, we determined through preliminary observations which latrine tree each of the focal animals would visit first after leaving the day-time resting tree. For the experiments, we introduced the feces in proximity to the identified latrine tree before sunset. For each experiment we used an approximately equal amount of feces. We started to record behavioral responses (i.e. loud calling, displaying, glandular scent-marking and sniffing) from the moment the focal individual entered the experimental latrine tree and continued behavioral observations for 30 min. In addition, we recorded the amount of time the animal spent in the latrine tree. We randomized the order in which we presented the three experimental treatments to the focal individuals. We only conducted one experimental treatment on one social unit during a single night. We removed the plastic sheets with the experimental feces immediately after each experiment.

Data analyses To determine whether animals discriminate between feces of their own, neighboring and strange social units, we used Friedman's ANOVA to test for differences between experimental treatments. We used rates of loud calling, sniffing, displaying and glandular scent-marking as measures of response intensity in males, but only rates of loud calling and sniffing in females. A new bout started when an individual interrupted the behavior for more than 5 seconds. In addition, we used the amount of time the animals spent in the experimental latrine tree as a response variable in both sexes. We based all calculations on the time the animals were in sight.

To establish the number and to investigate the distribution of latrines within the territories of the 7 social units, we calculated the size of individual annual home ranges with the Animal Movement extension of ArcView and plotted all recorded defecation/urination events. Since kernel densities do not require serial independence of observations, we did not correct for spatial autocorrelation (De Solla et al. 1999). However, we based our home range estimates on a constant time interval (i.e., 5 min) that is biologically meaningful, since it allows individuals to traverse their home range at maximum speed (Rooney et al., 1998). We calculated home range size from 95% fixed kernel home range utilization distributions (Worton 1989) using ad hoc smoothing (Silverman 1986). To establish whether defecation/urination occurred anywhere in an animal’s home range (i.e. random distribution of events) or were restricted to certain areas (i.e. clumped distribution of events) we used nearest neighbor analysis as implemented in the Animal Movement extension for ArcView (Hooge and Eichenlaub 1997). While R values of 1 indicate a random distribution, values of <1 and >1 indicate a tendency towards a clumped or a uniform distribution, respectively. Before running the analyses, we applied a small amount of random noise to the spatial location points of observed defecation/urination events to break ties between repeated observations at the same localities using the function ‘jitter’ of the R software (R Core Team 2011).

After ascertaining the spatial distribution of defecation/urination events via nearest neighbor analysis as being clumped, we established the number of latrines per territory by visual inspection of the spatial features in ArcView. Specifically, we considered a latrine as a cluster of defecation/urination events that were at a distance of up to 6 m of each other. We choose 6 m as a distance criterion, because this was the minimum distance at which a cluster of defecation/urination events would not disintegrate in a larger number of smaller, non-continuous latrines in close proximity to each other. When testing the various functional hypotheses of latrine use, we only considered defecation/urination events that were clearly associated with latrine visitations by removing all random defecation/urination events (i.e. single-use defecation sites that were not in proximity to a latrine; N = 32 or 5% of all defecation/urination events recorded).

To test the territory demarcation hypothesis, we established the number of defecation/urination events within the core vs. the boundary area as well as in the zones of home range overlap. We delineated core areas using a time maximizing function derived from kernel analyses (Vander Wal and Rodgers 2012).

To test the resource defense hypothesis with regard to defense of food, we investigated whether animals spent less time feeding within than outside the latrine area. We defined food patches as single feeding trees in which animals were observed feeding. Each food patch that was located within 6 m of a latrine tree was assigned as being part of the general latrine area. We calculated the relative proportion of feeding time within and outside the latrine area for each focal individual. In addition, we calculated the relative proportion of the number of food patches located within and without the latrine area. We calculated an index of feeding effort that allows accounting for the fact that the latrine area is smaller than the remaining home range area and, hence, innately can only contain a smaller number of potential food patches. We divided the proportion of foraging time within the latrine area by the relative proportion of the number of food patches located within the latrine area to calculate an index of feeding effort inside the latrine area. Likewise, we divided the proportion of foraging time outside the latrine area by the relative proportion of the number of food patches located outside the latrine area to calculate an index of feeding effort outside the latrine area. We compared feeding effort within and outside the latrine area using Wilcoxon signed-ranks test for each focal individual.

To test the resource defense hypothesis with regard to defense of sleeping sites, we investigated spatial dependence between defecation/urination sites and regular sleeping sites (i.e. sleeping trees that were used more than once by the focal animals). We conducted the analyses using the R package ‘spatstat’ (Baddeley and Turner 2005). We defined the union home range of all study individuals as the sampling window. We used the L-cross function to describe the dependence in bivariate point patterns using the independence approach (Dixon 2002). We used the inhomogeneous L-cross function to adjust for spatially varying intensity. For formal hypothesis testing, we computed simulation envelopes by pointwise Monte Carlo test. We used 99 simulations of CSR (complete spatial randomness) to compute envelopes. The theory of the Monte Carlo test requires the distance (r) to be fixed in advance for hypothesis testing (Baddeley and Turner 2005). We used a value of 6 m as a critical distance. Spatial dependence between points of two types occurs when events of each type are either closer (clustering) or farther away (inhibition) than expected under the assumption that the two processes are independent. Likewise, to test the mate defense hypothesis we investigated spatial dependence between defecation/urination sites and male glandular scent-marking sites.

To test the reproductive signaling hypothesis, we used linear mixed models (LMM) to estimate the effect of season on latrine use frequency (model 1). Since season may have a different effect on latrine use frequency in the two sexes, we included season, sex and their interaction in the model. We included individual identity nested within social unit as a random effect to control for pseudo-replication. In addition, to test the mate defense hypothesis, we used LMM to estimate the effect of intruder pressure on latrine use frequency in males (model 2). We considered observation nights in which focal males engaged in display behavior (i.e. branch bashing displays accompanied by loud calling) and/or placed glandular scent marks as nights with perceived intruder pressure. For each full-night observation we calculated the frequency of latrine use by dividing the number of latrine visits by the amount of time the focal animal was in sight. We included individual identity as a random effect to control for repeated observations. We controlled for the effect of the number of latrines within an individual's home range as well as for the effect of the type of social organization the individual lived in (i.e. pairs vs. one-male, two-female units). We transformed response variables using the function 'boxcox' of the package 'MASS' (Venables and Ripley 2002) and z-transformed the covariate (i.e. number of latrines; Schielzeth 2010).

We checked the distribution of the model residuals, plotted residuals against predicted values, conducted the Levène's test and correlated absolute residuals with fitted values to check model validity. We visually inspected qq-plots and plots of residuals vs. fitted values. None of the diagnostics indicated deviations from the assumptions of normality and homogeneity of residuals (Quinn and Keough 2002; Field et al. 2012). We calculated Variance Inflation Factors (VIFs) using the R function 'vif' of the package 'car' (Fox and Weisberg 2011) running a standard linear model with the random effect excluded from the predictors. VIFs indicated collinearity not to be an issue (largest VIF for model 1 = 2.03 and for model 2 = 1.35, respectively; Field et al. 2012). For influence diagnostics (Cook's distance, dfbetas) we used the R package 'influence.ME' for mixed effect models (Nieuwenhuis et al. 2012). The largest Cook's distance was only 0.14 for model 1. However, Cook's distances indicated some problems with model stability for model 2 (largest Cook's distance = 1.55). Similarly, unstandardized DFBeta values reached 1.15 for model 2, whereas values did not indicate any problems for model 1 (largest DFBeta = 0.68; Quinn and Keough 2002; Field et al. 2012). Running the second model without the influential case (male 4) did not lead to a different overall result, and hence, we report the results obtained for the complete dataset.

To test whether season or intruder pressure, respectively, had an overall effect on latrine use frequency we compared the full model to a model in which only these predictors were removed (i.e. season and its interaction with sex or perceived intruder pressure, respectively), using a likelihood ratio test. We fitted the models in R using the function ‘lmer’ in the package ‘lme4’ (Bates et al. 2012) using Maximum Likelihood rather than Restricted Maximum Likelihood to achieve more reliable P-values (Bolker et al. 2008). We derived P-values for the individual effects based on Satterthwaite approximation for denominator degrees of freedom by using the function ‘summary’ of the R package ‘lmerTest’ (Kuznetsova et al. 2014). We considered $P \leq 0.05$ as statistically significant.

Results

General latrine behavior Animals remained on average 5.8 ± 9.4 min (mean ± SD; N = 678) in trees in which they defecated/urinated. Similarly, they spent in total only 6% of the total observation time they were in sight in trees in which they defecated/urinated. They lifted their tail to defecate and urinate while clinging to tree trunks. While the feces dropped to the ground, the urine dripped down the main trunk of the tree and left visible stains even once the urine was dried. While *Lepilemur* feces were not very odorous, at least to the human nose, urine was characterized by a distinct species-specific odor. We could observe the focal animals on two occasions to lick and on 26 occasions to sniff the bark of a tree. On 15 of these occasions this behavior occurred in the general latrine area and on six occasions in an identified latrine tree. Outside the observation period, we could observe a male to sniff a wet urine stain that was deposited 8 min earlier by a female in the latrine. In addition, we could observe the animals on four occasions to lower themselves to less than 1 m above the ground in a latrine tree to inspect the ground.

Experimental translocation of feces The time spent in the experimental latrine ranged between 11 and 80% (mean ± SD: 29 ± 23) of the observation time in females and between 11 and 39% (20 ± 7) in males. Rates of loud calling ranged between 0 and 2 bouts/h in females (0.14 ± 0.55) and males (0.27 ± 70). While we could not observe females to engage in sniffing, rates of sniffing ranged between 0 and 8 bouts/h in males (1.21 ± 2.49). We could not observe males to engage in display behavior during the experiment, but rates of scent-marking ranged between 0 and 2 bouts/h (0.54 ± 0.92). Response intensity did not differ significantly among the three experimental treatments in either males or females. More precisely, the amount of time spent in the latrine tree (females: $\chi^2 = 1.3$, df = 2, $P = 0.522$; males: $\chi^2 = 5.7$, df = 2, $P = 0.058$), rates of loud calling (females: $\chi^2 = 0.3$, df = 2, $P = 0.861$; males: $\chi^2 = 0.3$, df = 2, $P = 0.861$), sniffing (females: $\chi^2 = 0.0$, df = 2, $P = 1$; males: $\chi^2 = 1.2$, df = 2, $P = 0.549$), displaying (males: $\chi^2 = 0.0$, df = 2, $P = 1$) and scent-marking (males: $\chi^2 = 1.2$, df = 2, $P = 0.549$) did not differ significantly among treatments.

Spatial distribution of defecation/urination events Union home range size (95 % Kernel estimates) for the seven social units ranged between 0.28 and 0.47 ha (mean ± SD: 0.38 ± 0.07 ha, N = 7). Nearest neighbor analyses of the locations of defecation/urination events computed R-values ranging between 0.15 and 0.48 for the union home ranges. Within all seven union home ranges the spatial distribution of the defecation/urination events differed significantly from a random spatial distribution ($P < 0.001$, N = 7), with a tendency towards clumping as opposed to towards an even distribution (Table 1). We identified 3 to 4 latrines in each union home range (Fig. 1).

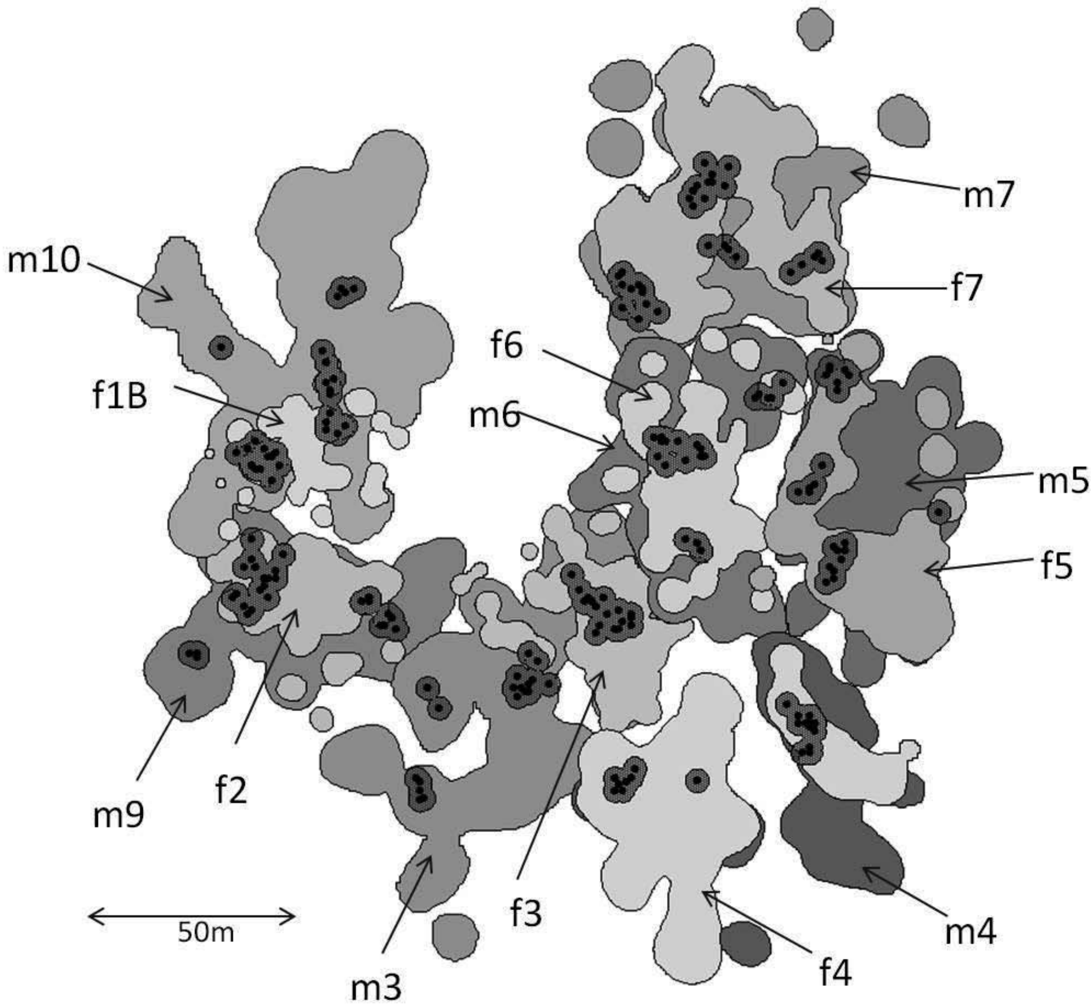

Fig. 1 95% kernel annual home ranges for individual adult males (m) and females (f) of *Lepilemur leucopus* at Berenty between October 2011 and October 2012 as well as the spatial arrangement of the latrines within the home ranges. Dots represent individual latrines trees whereas the shaded areas represent a contagious buffer of 3 m around individual latrine trees to distinguish discrete latrines. Home ranges of pair partners overlap (Sex: m = male, f = female).

Table 1 Spatial distribution of observed defecation/urination events within the union home ranges of seven social units of *Lepilemur leucopus* based on nearest neighbor analysis.

Social Unit	# defecation events	Z-value	R-value	P-Value
1	100	-13.59	0.22	<0.001
2	135	-16.73	0.17	<0.001
3	112	-12.75	0.23	<0.001
4	72	-8.09	0.48	<0.001
5	86	-11.34	0.35	<0.001
6	115	-17.20	0.15	<0.001
7	90	-13.91	0.22	<0.001

Territory demarcation hypothesis We recorded a total of 678 defecation/urination events. Using the time maximization function, core areas of individual ranges were delineated by 65 % isopleths. Union core areas (65 % Kernel estimates) represented 26 ± 6 % (range: 20 - 37 %, N = 7) of the union home ranges (95 % Kernel estimates) of the social units. However, the majority of defecation/urination events (mean ± SD: 82 ± 7 %, range: 72 - 94 %, N = 7) were located within the small union core areas of the social units, so that the density of defecation/urination events was significantly higher in the core area (mean ± SD: 875 ± 391 events/ha) compared to the remaining home range are (72 ± 54 events /ha; Wilcoxon signed-rank test: V = 28, P = 0.016, N = 7). The overlap zones comprised only 1.35% of the union of all individual home ranges. None of the defecation/urination events were located within overlap zones of neighboring territories.

Resource defense hypothesis The relative proportion of foraging time within the latrine area ranged between 22 and 43% (mean ± SD: 31 ± 7 %, N = 14). The relative proportion of the number of patches located within the latrine area ranged between 23 and 46% (34 ± 7 %). The index of feeding effort inside the latrine area ranged between 0.7 and 1.1 (0.9 ± 0.1) and between 0.8 and 1.1 (0.9 ± 0.1) for the feeding effort outside the latrine area. Feeding effort within the latrine area did not differ significantly from the feeding effort outside the latrine area (Wilcoxon signed-ranks test: V = 56, N = 14, *P* = 0.851). The animals spent only between 2 and 14 % (mean ± SD: 7 ± 4 %, N = 14) of the total feeding time eating in identified latrine trees. While we could record a total number of 1584 food patches throughout the study, animals were only seen to defecate/urinate in 79 of them. In addition, animals were observed to forage in only 41% ± 11% (range: 24 to 55%, N = 14) of the identified latrines trees.

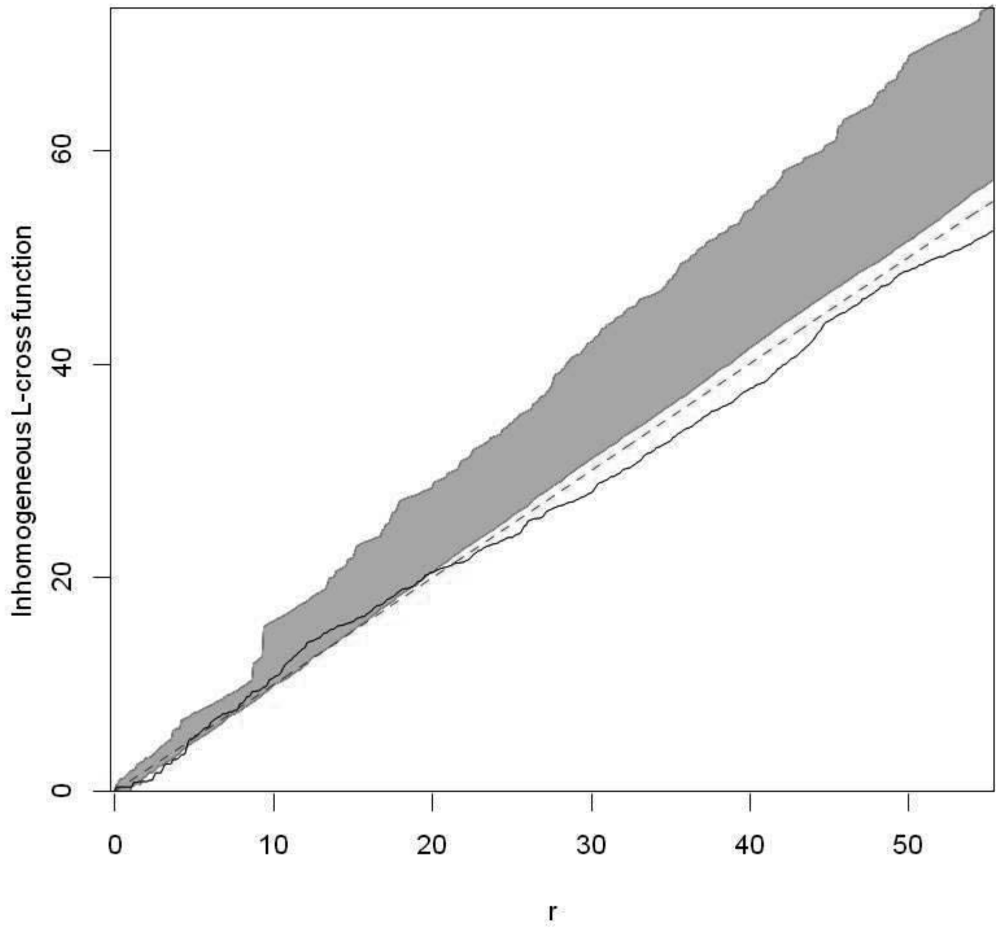

Fig. 2 Estimated inhomogeneous L-cross function and envelopes for the bivariate point pattern consisting of defecation/urination sites and sleeping trees. The solid line indicates the empirical L-cross function, the dotted line the theoretical value for complete spatial randomness (CSR) and the grey band the envelope from 99 simulations and r is the distance argument.

The number of repeatedly used sleeping trees ranged between 5 and 10 (mean ± SD: 7 ± 2) for the 7 social units. None of the latrine trees served as a sleeping tree. The computed empirical homogenous L-cross function fell within the simulation envelop at the critical distance of 6 m, indicating spatial independence between defecation/urination and sleeping sites (Fig. 2).

Social bonding hypothesis Regarding the social units consisting of one adult male and two adult females (unit 1 and 3), all latrines located within the common range of the focal male and focal female were shared by both adult individuals. All latrines within the home ranges of social units consisting of one male and one female were shared by both pair-partners, with the exception of social unit 2 where only 2 of 3 latrines were shared. We only once saw a focal individual (m6) to visit a neighbor's latrine (unit 7). In addition, we recorded 47 defecation/urination events by un-collared individuals. 46 of these defecation/urination events were associated with an identified latrine. In 41 of these cases, it was the offspring, which ranged within the parental territory. In 6 cases it was the second adult un-collared female of unit 1 and 3, respectively. In total, we could observe co-use by un-collared individuals in 18 out of 25 identified latrines.

Reproductive signaling hypothesis Latrine use frequency (number of latrine visitations/h) equaled 0.58 ± 0.25 (mean ± SD; N = 25) during the early wet, 0.48 ± 0.21 (N = 26) during the late wet, 0.48 ± 0.19 (N = 28) during the early dry and 0.55 ± 0.19 (N = 28) during the late dry season. The result of the LMM to estimate the effect of season on latrine use frequency (model 1) indicated that the full model containing the effects of season and its interaction with sex was not significantly better in explaining the data than the null model (likelihood ratio test: $\chi^2 = 8.639$, df = 7, $P = 0.279$).

Mate defense hypothesis During 25 observations nights, we observed focal males to place anogenital scent marks and during 21 nights they engaged in branch bashing and vocal displays. One or both of these behaviors were recorded during 37 out of 51 observation nights on adult males. The result of the LMM to estimate the effect of perceived intruder pressure (as indicated by display and scent marking behavior) on latrine use frequency in males (model 2) showed that the full model was significantly better in explaining the data than the null model (likelihood ratio test: $\chi^2 = 6.3327$, df = 1, $P = 0.012$). Latrine use frequency was significantly increased in males during nights of perceived intruder pressure (mean frequency of latrine visitation ± SD: nights with intruder pressure = 0.60 ± 0.27 latrine visitations/h, nights without intruder pressure = 0.46 ± 0.18; P = 0.011; Table 2). In total, we recorded 50 scent-marking events by the 7 focal males. 32 of these scent marks were placed in an identified latrine tree. At the critical distance of 6 m the computed empirical inhomogeneous L-cross function fell above the simulation envelop, indicating spatial dependence (attraction) between latrines and scent-marking locations (Fig. 3).

Table 2 Effects of perceived intruder pressure, number of latrines and social organization on latrine use frequency in male *Lepilemur leucopus* (LMM).

Fixed Factor	β	SE	df	t	P
Intercept	1.019	0.002	9.55	473.012	NA
Intruder pressure perceived (yes)	-0.005	0.002	44.44	-2.658	0.011
Number of latrines	0.003	0.002	6.69	1.474	0.186
Social organization (1 ♂ & 2 ♀)	-0.007	0.004	7.49	-1.672	0.136

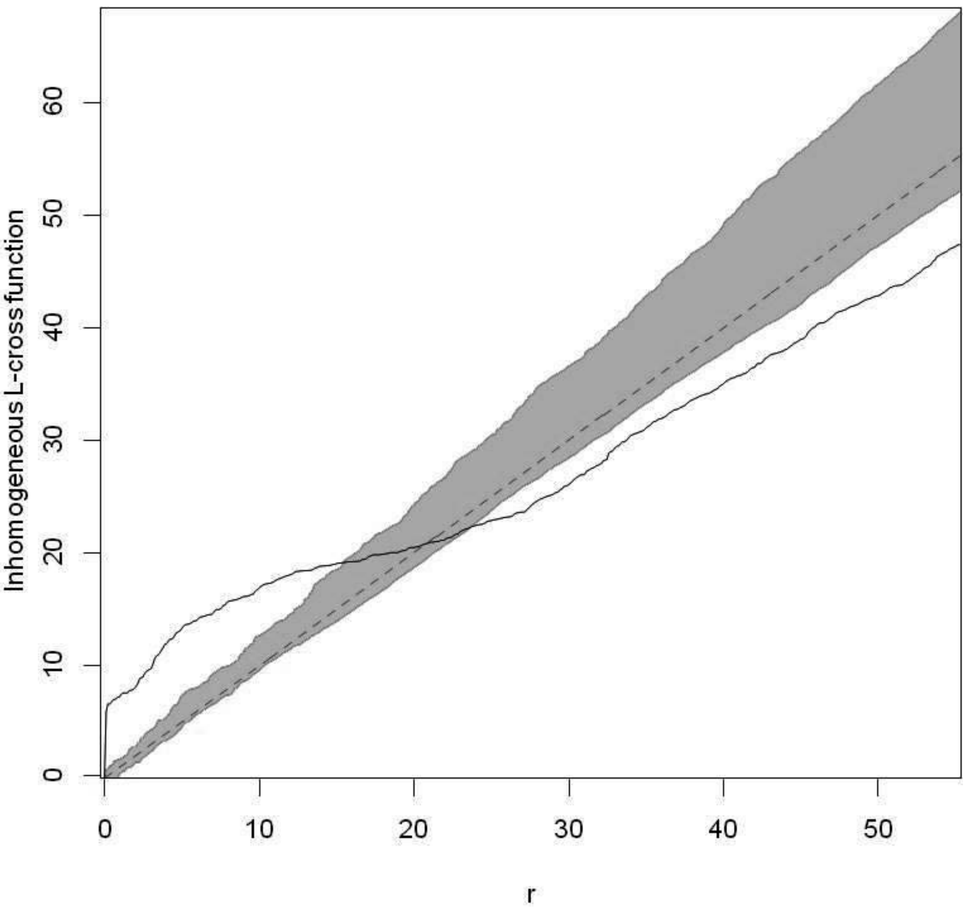

Fig. 3 Estimated inhomogeneous L-cross function and envelopes for the bivariate point pattern consisting of defecation/urination and scent marking sites. The solid line indicates the empirical L-cross function, the dotted line the theoretical value for complete spatial randomness (CSR) and the grey band the envelope from 99 simulations and r is the distance argument.

Discussion

Our study revealed that defecation/urination events were highly clustered in space, resulting in 3 - 4 latrines with terrestrial accumulations of feces in each territory. The study animals spent only a notably short time in trees they visited for defecation/urination and, therefore, the formation of latrines is not a mere by-product of animals remaining for a considerable time in a few preferred resting trees (Charles-Dominique and Hladik 1971; Schilling 1979). The number and locations of latrines were stable throughout the study period. We tested whether terrestrial accumulations of feces in an arboreal species can be considered to have an olfactory signaling function. We found no support for this notion and conclude that urine, which is more accessible to the animals for olfactory investigation, is the more important latrine component in this species. Additionally, we found empirical support for the hypotheses that latrines function in social bonding and mate defense, but a potential function in territory demarcation, resource defense and signaling of reproductive state could not be shown. Below, we discuss these findings in relation to the social system of *L. leucopus* and in light of available data for other latrine-using mammals.

Experimental translocation of feces Most species that exhibit latrine use are terrestrial, and feces are therefore assumed to be salient sources of olfactory signals. However, *L. leucopus* did not react differently to experimentally introduced feces from neighboring or strange social units, compared to feces from familiar animals. In contrast, river otters (*Lontra canadensis*) investigate foreign scat more than local one when added to latrines (Oldham 2009). Brown brocket deer (*Mazama gouazoubira*) investigate introduced dung from unknown individuals of the same sex significantly more than their own dung, and males counter-mark introduced dung with a greater frequency than females (Black-Decima and Santana 2011). Badgers (*Meles meles*) respond more intensely towards foreign feces, and the response is greatest during the breeding season (Palphramand and White 2007). Among primates, only *Cheirogaleus* spp. produce arboreal latrines by smearing feces on branches during repeated walking defecation, resulting in a fecal accumulation adhering to the branch (Petter 1962). In arboreal species, such as *L. leucopus*, terrestrial latrines may serve as an optical signal (Irwin et al. 2004). Moreover, urination above ground facilitates dispersal of the odor by wind, and increases the evaporating surface as the urine drips downward (Sillero-Zubiri and Macdonald 1998). Because urine marking is an ancestral behavior in strepsirrhine primates (Delbarco-Trillo et al. 2011), more experimental studies of urine communication in solitary and nocturnal species are called for.

Social bonding Scent-marks may function as self-advertisement and simply signal an individual’s presence and identity to mates, family members, neighbors, and/or intruders (Eisenberg and Kleiman 1972; Peter and Mech 1975; Wolff et al. 2002), and latrines may serve as information exchange centers of individual-specific information (Darden et al. 2008; Black-Decima and Santana 2011). Latrines are maintained by all individuals of a social unit in *L. leucopus*. In contrast, in European badgers (*Meles meles*), a species in which latrines function mainly in territorial defense and demarcation, sexually immature juveniles rarely defecate/urinate at latrines (Brown et al. 2009). Latrines have been suggested to help maintaining social bonds in some ungulates such as steenbok (*Raphicerus campestris*), oribi (*Ourebia ourebi*) and dikdik (*Madoqua kirkii*; Kingdon 1982; Apio et al. 2006). Behaviors that facilitate familiarity and, hence, intra-group recognition may be especially important in solitary foragers with minimal direct social contact between individuals (Dröscher and Kappeler 2013). These observations are in contrast to observations on swift foxes (*Vulpes velox*), where mated pairs exhibit high levels of den sharing that allows the exchange of information within the pair and to maintain the pair bond. Thus, latrines are not considered important for intra-pair communication and maintenance of social cohesion in *V. velox* (Darden et al. 2008). Latrine locations within the core areas of *L. leucopus* also support the idea that they function in social bonding since this form of placement should be particularly suited for information exchange between group members (Wronski et al. 2013).

In Coquerel's sifakas (*Propithecus coquereli*) the quality of the pair bond of breeding pairs is reflected in their olfactory signals by chemical convergence, possibly due to similar volatile production by shared microbial communities obtained through the exchange of odorant-producing microbes for example via overmarking (Greene and Drea 2014). Similarly, anal gland secretions that coat or saturate badger feces seem to have a group-specific chemical composition (Davies et al. 1988). Analogously, convergence in vocal signals facilitates group and pair cohesion in some primate and avian species (Geissmann and Orgeldinger 2000; Tyack 2008; Sewall 2009; Candiotti et al. 2012). Sportive lemurs not only exchange chemical but also acoustic signals. While pairs of the Milne Edwards' sportive lemur (*L. edwardsi*) coordinate loud calls in duets, perhaps to strengthen pair bonds (Méndez-Cárdenas and Zimmermann 2009), neither red-tailed sportive lemurs (*L. ruficaudatus*; Fichtel and Hilgartner 2013) nor *L. leucopus* exchange vocalizations in coordinated duets. In addition, males and females of *L. leucopus* produce sex-specific loud calls and thus are not available for vocal convergence. It therefore remains to be determined what exactly social bonding entails in different species and which aspects of it can be communicated in different modalities.

Mate defense Latrines may play a role in mate defense by advertising the commitment of resident males to defend co-resident females (Roper et al. 1986; Jordan et al. 2007). We found that male latrine use frequency increased during nights of perceived intruder pressure. Likewise, latrine use frequency increases in meerkats (*Suricata suricatta*) when prospecting males are present (Jordan et al. 2007). In European badgers (*Meles meles*) males visit boundary latrines more often than females (Roper et al. 1993; Stewart et al. 2001), presumably to signal their commitment to guarding females of their own social group (Roper et al. 1986). Similarly, male brown brocket deer defecate/urinate more often after detecting dung from unknown individuals near one of their latrines. By re-marking their latrine, residents are thought to affirm their dominant or resident status (Black-Decima and Santana 2011).

We do not have systematic data on the behavior of intruders. However, outside the focal observation period we could observe a resident and a roaming male to repeatedly visit the same latrine tree to defecate, urinate and place glandular scent marks. Male scent-marking is linked to intra-sexual competition in several species (e.g. *Microtus* spp.: Jannett 1986; *Myocastor coypus*: Gosling and Wright 1994; *Lemur catta*: Kappeler 1998) and by strategically placing anogenital scent marks in latrines, which are composite olfactory signals of all members of a group, males of *L. leucopus* may also signal their competitive ability and willingness to defend their social unit to intruders (Rich and Hurst 1998).

Signaling of reproductive state Males are often able to detect chemical cues in female urine and/or feces related to reproductive state (Rasmussen et al. 1982; Ghosal et al. 2012; Archunan and Rajagopala 2013). Contrary to our predictions, frequency of latrine use in *L. leucopus* did not increase during the mating season. In contrast, genets (*Genetta genetta*) exhibit increased scat deposition at latrine sites during the mating period (Barrientos 2006). Similarly, latrine visitation peaks during the mating season in *M. meles* (Pigozzi 1989; Roper et al. 1993). While females may scent-mark to advertise their reproductive state to attract males (Converse et al. 1995; Heymann 1998; Kappeler 1998), males may mask female scent to hide their estrous condition from competing males or to advertise their presence to other males (Trumler 1958; Klingel 1974; Rich and Hurst 1998; Lewis 2005; Jordan et al. 2007). Although we cannot exclude the possibility that reproductive status may be communicated at latrine sites in *L. leucopus*, the function of latrine use does not appear to be specifically related to male attraction or to over-marking signals of estrous females, since neither females nor males increased latrine use frequency during the mating season. However, estrus in sportive lemurs is seasonal and short (Randrianambinina et al. 2007; Hilgartner et al. 2008) and any effect may have been concealed by our method of data collection, because we did not follow pairs when females were apparently in estrus.

Territory demarcation Urine and feces are common, readily available materials and many mammals use them to demarcate their territories or home ranges (e.g. *Meles meles*; Pigozzi 1989; *Panthera tigris*: Smith et al. 1989; *Ourebia ourebi*: Brashares and Arcese 1999). We found that the majority of defecation/urination events were localized within the core areas of the territories, even though *L. leucopus* is highly territorial (Dröscher and Kappeler 2013). However, where latrines cannot be economically maintained because territory borders are too long, they should be placed in the center of the territory (Jordan et al. 2007). For example, brown hyenas (*Hyaena brunnea*) exhibit boundary marking when they live in small territories but display center marking if they inhabit large territories (Mills and Gorman 1987). Since territory size in *L. leucopus* is only 0.3 ha and individuals can easily traverse their territories in no more than 5 minutes, it is unlikely that territory size in this species would preclude a border marking strategy. In *M. meles* latrine use is primarily concentrated along territory boundaries and these are shared by members of the same and neighboring groups (Kilshaw et al. 2009) and are visited mainly by males (Roper et al. 1993). Besides boundary latrines, badgers also use hinterland latrines, which are visited by both sexes (Roper et al. 1993). In *L. leucopus* all latrines were visited by both pair-partners. Furthermore, we could observe only once a focal animal to visit a neighboring latrine, indicating that latrines in *L. leucopus* are not used for inter-group information transfer to monitor occupancy of surrounding territories (Jordan et al. 2007). Instead of latrines, sportive lemurs seem to use vocalizations to signal occupancy and to regulate spacing within and between social units (Rasoloharijaona et al. 2006; Fichtel and Hilgartner 2013).

Resource defense Resources such as resting sites (Goszczynski 1990; Branch 1993; Brady and Armitage 1999) and food trees may be marked to identify ownership and to deter conspecifics (Kruuk 1992; Miller et al. 2003). Contrary to our prediction, spatial locations of latrine trees and sleeping trees were spatially independent from each other, notwithstanding the fact that sportive lemurs only use a few selected sleeping sites and appropriate sleeping sites are limited, potentially leading to competition within or between social units (Rasoloharijaona et al. 2003, 2008). Establishing ownership of sleeping sites, therefore, may be beneficial to individuals by ensuring protection from predators or adverse climatic conditions (Franklin et al. 2007). For example, weasel sportive lemurs (*L. mustelinus*) gouge trees after leaving sleeping sites and before moving around, suggesting that they use non-nutritive tree gouging to display ownership of sleeping sites (Rasoloharijaona et al. 2010). Tree gouging behavior is absent in *L. leucopus* and if latrines were to function instead for sleeping site defense one would expect latrine trees to be in proximity to sleeping trees. Conversely, scent-marks can potentially be exploited by predators to localize prey (Cushing 1984; Viitala et al. 1995), and an intentional placement of latrine trees in proximity to sleeping trees would seem to be disadvantageous in terms of predator attraction. In addition, animals may mark food trees as a means of asserting ownership of food resources.

Communal use of latrines in *L. leucopus* rejects the idea that they are used to signal resource use among members of a social unit. In contrast, otters (*Lutra lutra*) deposit spraints (i.e. token feces) to signal the use of feeding areas exploited by each individual (Kruuk 1992). Alternatively, members of a social unit of *L. leucopus* may use latrines to signal to other social units their willingness to defend their food resources. However, *L. leucopus* did not preferentially defecate/urinate in food trees since animals were observed to defecate/urinate in only 5% of all identified food patches and to feed in less than 50% of the identified latrine trees. In addition, the fact that individual feeding effort was equally distributed within and outside the latrine area indicates that latrines are not used to mark important feeding areas. These results are in line with the observation that *L. leucopus* exhibits low dietary selectivity, rely on the most common food species and rarely engage in conflict over food neither within nor between social units (Dröscher and Kappeler 2014).

Conclusions

Latrines are found in solitary, pair- and group-living mammals (Table 3). Latrine use appears to be common among species that are nocturnal, exhibit a dispersed social system and are territorial. Since many species do not just defecate, but often also urinate and deposit glandular secrets at latrine sites, these signals may function to convey more than one message. Especially in arboreal species with terrestrial accumulations of feces, urine may be of greater importance for chemical signaling than feces. Despite comparative data being sparse, a general pattern emerges that latrines are used in intra-specific olfactory communication in many cases. Although not restricted to nocturnal species, latrine use may facilitate communication in species with limited habitat visibility. Furthermore, latrines can be considered to be economical in species with low inter-individual cohesion, since individuals can benefit from predictable areas for information exchange. Notwithstanding the fact of being more common among territorial species, latrine use does not appear to necessarily function in territory demarcation. Clearly, more experimental studies are required to investigate the relative importance and functions of different modes of olfactory signaling at latrine sites.

Table 3 Overview of mammalian latrine users and species-specific attributes such as habitat use (T = terrestrial, A = arboreal, AQ = aquatic), period of activity (D = diurnal, N = nocturnal, C = crepuscular), social organization (S = solitary, P = pair, G = group) and cohesiveness during foraging (G = gregarious, D = dispersed) as well as suggested function of latrine use (1 = territory demarcation, 2 = resource defense, 3 = centers of information exchange, 4 = reproductive signaling, 5= mate defense/intrasexual competition, 6 = signaling of social status).

Order	Species	Common name	Habitat	Activity	Social organization	Cohesion	Territoriality	Function	Reference
Artiodactyla	Alcelaphus buselaphus	Hartebeest	T	D	G	G	yes		Gosling 1974
	Cervus eldi	Eld's deer	T	N/C	G	G	no		Wemmer and Montali 1988
	Damaliscus korrigum	Topi	T	N/D	G	G	yes	1	Gosling 1987
	Gazella dorcas	Dorcas gazelle	T	N/D/C	P/G	G	yes		Essghaier and Johnson 1981
	Gazella gazella	Mountain gazelle	T	D	G	G	yes		Wronski and Plat 2010
	Gazella granti	Grant’s gazelle	T	N/D	G	G	yes	1	Estes 1991
	Gazella thomsoni	Thomson’s gazelle	T	N/D	G	G	yes		Walther 1978
	Hydropotes inermis	Water deer	T	C	S	D	yes		Sun et al. 1994
	Lama guanicoe	Guanaco	T	D	G	G	yes		Henriquez 2004
	Madoqua guentheri	Guenther's dik-dik	T	N/D	P	G	yes	1	Ono et al. 1988
	Madoqua kirkii	Kirk's dik-dik	T	N/D	P	G	yes	3	Hendrichs and Hendrichs 1971
	Mazama americana	Red brocket deer	T	N/D	S/P	D	yes		Rivero et al. 2004
	Mazama gouazoubira	Brown brocket deer	T	N	S	D	yes	3,5	Black-Decima and Santana 2011
	Moschus chrysogaster	Alpine musk deer	T	N	G	D	yes		Qureshi et al. 2004
	Moschus moschiferus	Siberian musk deer	T	N	G	D	yes		Green 1987
	Muntiacus muntjak	Indian muntjac	T	N/D	S	D	yes	1	Dubost 1971
	Muntiacus reevesi	Chinese muntjac	T	N/D	S	D	yes	1	Dubost 1970
	Oreotragus oreotragus	Klipspringer	T	D	P	G	yes	1	Roberts and Lowen 1997
	Ourebia ourebi	Oribi	T	D	S/P/G	G	yes	1,3	Brashares and Arcese 1999
	Pudu puda	Southern pudu	T	N/D	S	D	yes		MacNamara and Eldridge 1987
	Raphicerus campestris	Steinbuck	T	D	P	D	yes	3	Kingdon 1982
	Tragelaphus scriptus	Bushbuck	T	N/C	G	D	yes	3,4	Wronski et al. 2006
	Vicugna pacos	Alpaca	T	D	G	G	yes		McGregor and Brown 2010
Perissodactyla	Ceratotherium simum	White rhinoceros	T	N/D	S/G	G	yes		Owen-Smith 1975
	Diceros bicornis	Black rhinoceros	T	N/D	S	D	yes		Linklater et al. 2013
	Rhinocerus unicornis	Indian rhinoceros	T	N/D	S	D	yes		Dinerstein and Wemmer 1988
	Tapirus terrestris	South American tapir	T	N/C	S	D	yes		Fragoso et al. 2003
Carnivora	Bassariscus astutus	Ring-tailed cat	T	N/C	S	D	yes		Barja and List 2006
	Canis aureus	Golden jackal	T	N/D	G	D	yes		Macdonald 1980
	Canis latrans	Coyote	T	N/D	S/P/G	D,G	yes		Ralls and Smith 2004
	Canis simensis	Ethopian wolf	T	D	G	D	yes		Sillero-Zubiri and Macdonald 1998

Order	Species	Common name	Habitat	Activity	Social organization	Cohesion	Territoriality	Function	Reference
	Civettictis civetta	African civet	T	N	S	D	yes		Bearder and Randall 1978
	Crocuta crocuta	Spotted hyena	T	N	G	G	yes		Gorman and Mill 1984
	Genetta genetta	Common genet	T, A	N	S/P	D	yes	4,5	Barrientos 2006
	Hyaena brunnea	Brown hyena	T	N	G	G	yes	1	Mills et al. 1980
	Hyaena hyaena	Striped hyena	T	N	G	D	yes		Macdonald 1980
	Lontra canadensis	River otter	T, AQ	N/C	G	G	yes	6	Rostain et al. 2004
	Martes martes	Pine marten	T,A	N	S	D	yes		Barja et al. 2011
	Meles meles	European badger	T	N/C	G	D	yes	1,2,4,5	Roper et al. 1993; Balestrieri et al. 2011
	Nyctereutes procyonoides	Raccoon dog	T	N	P	D	no	3	Ikeda 1984
	Procyon lotor	Northern raccoon	T	N	G	D	variable		Brown and Macdonald 1985
	Proteles cristatus	Aardwolf	T	N	P	D	yes		Nel and Bothma 2002
	Pteronura brasiliensis	Giant otters	T, AQ	D	G	G	yes		Leuchtenberger and Mourão 2009
	Suricata suricatta	Meerkats	T	D	G	G	yes	1,5	Jordan et al. 2007
	Urocyon cinereoargenteus	Gray fox	T	N/C	P	D	yes		Trapp 1978
	Vulpes macrotis	Kit fox	T	N	P	D	yes		Ralls and Smith 2004
	Vulpes velox	Swift fox	T	N	P	D	yes	1	Darden et al. 2008
Dasyuromorphia	Dasyurus geoffroii	Western quoll	T	N/C	S	D	yes		Serena and Soderquist 1989
	Dasyurus hallucatus	Northern quoll	T	N	S	D	no		Oakwood 2002
	Dasyurus maculatus	Tiger quoll	T	N	S	D	yes		Ruibal et al. 2010
	Myrmecobius fasciatus	Numbat	T	D	S	D	yes	1	Hogan et al. 2013
	Sarcophilus harrisii	Tasmanian devil	T	N	S	D	no		Pemberton 1990
Diprotodontia	Petropseudes dahli	Rock-haunting possum	T	N	P	G	yes		Runcie 2004
Hyracoidea	Dendrohyrax arboreus	Southern tree hyrax	A	N/D	S/P	D	yes		Milner and Harris 1999
	Dendrohyrax validus	Eastern tree hyrax	A	N	?	D	yes		Topp-Jørgensen et al. 2008
	Heterohyrax brucei	Yellow-spotted rock hyrax	T	D	G	G	yes		Barry and Shoshani 2000
	Procavia capensis	Rock hyrax	T	D	G	G	yes		Meadows et al. 2010
Lagomorpha	Oryctolagus cuniculus	European rabbit	T	N	G	G	yes		Sneddon 1991
Primates	Alouatta caraya	Black howler monkey	A	D	G	G	yes		Bravo and Zunino 2000
	Alouatta seniculus	Red howler monkey	A	D	G	G	yes		Julliot 1996
	Ateles geoffroyi	Geoffroy's spider monkey	A	D	G	G	yes		González-Zamora et al. 2012
	Cheirogaleus major	Greater dwarf lemur	A	N	P	D	yes		Petter 1962
	Cheirogaleus medius	Fat-tailed dwarf lemur	A	N	P	D	yes		Petter 1962
	Hapalemur griseus	Lesser bamboo lemur	A	D	G	G	yes	2,4,5	Irwin et al. 2004
	Hapalemur meridionalis	Southern lesser bamboo lemur	A	D	G	G	yes	1,2	Eppley and Donati 2010
	Lagothrix lagotricha	Woolly monkey	A	D	G	G	yes		Yumoto et al. 1999
	Lepilemur leucopus	White-footed sportive lemur	A	N	P	D	yes	3,5	this study
	Lepilemur wrightae	Wright's sportive lemur	A	N	P	D	yes	2,4,5	Irwin et al. 2004
Rodentia	Arvicola terrestris	Water vole	T, AQ	N	S	D	yes	4	Woodroffe et al. 1990

CHAPTER 4

Nutritional consequences of folivory in a small primate: effects of season and reproduction on nutrient balancing

With Jessica M. Rothman, Jörg U. Ganzhorn and Peter M. Kappeler

in preparation for submission

Abstract

Small-bodied folivores are rare because processing leaves often requires extensive gut adaptations and lengthy retention times for fiber fermentation. However, in the spiny forests of Southern Madagascar, the < 1 kg nocturnal white-footed sportive lemurs (*Lepilemur leucopus*) persist on a diet of solely vegetation. We investigated how extrinsic (i.e. seasonality in temperature and food availability) and intrinsic factors (i.e. reproductive state) influence nutrient intake and explored how nutrient and energy needs are met in this small-bodied folivorous primate. We conducted full night focal follows across seasons and analyzed nutrients in foods eaten by males and females. We estimated digestible protein content, as this is a biologically more meaningful measure than crude protein. Protein intake was constant across seasons, while non-protein energy intake increased with decreasing ambient temperatures. Males and females did not differ in their nutrient or energy intake irrespective of female reproductive state. We conclude that animals prioritize protein over non-protein intake as dietary protein is in limited supply and that thermoregulation poses higher energetic costs than reproduction in this species. While lactating females did not increase their protein intake, the relative protein content of the diet was highest during the lactation period, indicating that the balance of non-protein to protein energy intake may be more important than absolute intakes. Dry matter intake was high compared to other folivorous primates, indicating that *L. leucopus* follows an intake opposed to an efficiency strategy to meet its energy requirements.

Introduction

Folivores subsist on a diet that is considered to be of low quality as leaves are generally high in structural carbohydrates that are difficult to digest (Milton 1979; Cork et al. 1983). Only few vertebrates use leaves as food, and for most of those leaves constitutes only a minor dietary compenent (McNab 1978). Folivory, as a dietary specialization, has evolved independently in some ungulate (Janis 2008), sloth (Montgomery and Sunquist 1978), marsupial (Kanowski et al. 2003), rodent (Muul and Liat 1978) and primate species (Clutton-Brock 1977). Based on Kay's threshold hypothesis, body size imposes an upper limit on insectivory and a lower limit on folivory, while frugivorous species tend to be at intermediate body size (Kay 1984). Large body size is the primary morphological adaption to folivory as larger gastro-intestinal surface area and longer digestion time allow maximum nutrient absorption (Chivers and Hladik 1980). On the physiological level, hypometabolism (Kleiber 1961) can be seen as an energy-conserving adaptation to a diet that is deviant for a given body size (Kurland and Pearson 1986). Similarly, cecotrophy is a digestive adaptation to metabolic constraints imposed by small body size (Hörnicke and Björnhag 1980). Most arboreal folivores are large, usually 1 to 5 kg, to handle large quantities of food of low caloric and nutritional density (McNab 1978). Folivory is rarely observed in small-bodied primate species (< 1 kg) and little is known about whether or how these can meet their energy requirements through diet selection.

Energy needs and nutrient requirements are influenced by intrinsic factors, such as reproductive state, as well as by extrinsic factors such as seasonality in temperature and food availability due to climate variability. Energetic costs in sexually monomorphic mammals are likely to be greater for females who bear the costs of gestation and lactation in addition to the costs of body maintenance (Gittleman and Thompson 1988; Key and Ross 1999). Lactation is the most energetically expensive reproductive state (McCabe and

Fedigan 2007) and if sexes differ in the quantity and/or composition of resources they require, difference should become increasingly apparent as gestation and lactation progress (Morehouse et al. 2010). Although previous studies have demonstrated that males and females may differ in their diets (Grassi 2002; Vasey 2002; Doran-Sheehy et al. 2009; Hartwell et al. 2014), information on sex-specific nutritional intake is scarce (see e.g., Rothman et al. 2008; Gould et al. 2011).

Climate can have a direct influence on the physiology and behavior of organisms through changes in ambient temperatures (Dearing et al. 2008; Terrien et al. 2011). While diurnal species may be seasonally affected by heat-stress (Hill 2006), nocturnal species may be seasonally affected by cold-stress (Müller 1979; Nash 1998). Moreover, the relatively low basal metabolic rate of many strepsirrhine primates makes it difficult for them to deal with cool environments (Müller 1979). While thermal stress can be a significant constraint on primate activity patterns (Nash 1998; Fernandez-Duque 2003; Erkert and Kappeler 2004; Vasey 2005), the influence of thermoregulatory demands on nutrient requirements is not well understood.

Climate can have an indirect effect on the life of animals through its influence on the phenology of the plant community and, hence, the quantity and quality of available food items (van Schaik & Brockman 2005). Leaves have traditionally been considered as a rather invariant and abundant resource in constant supply. However, it has been shown that primates prefer young over mature leaves (Chapman et al. 2004), and that the amplitude of leafing seasonality can be greater than that of fruiting (Hemingway 1998). Thus, seasonal shifts in leaf production could have a profound effect on folivores that rely on young leaves.

We choose the white-footed sportive lemur (*Lepilemur leucopus*) as a study species to investigate the impact of seasonal temperature variability, seasonal food characteristics and reproductive state on energy and nutrient intake. Their geographic range is confined to southern Madagascar, where hot wet summers alternate with cold dry winters (Jolly et al. 2006). They are seasonal breeders that time breeding so that offspring are born and weaned during periods of food abundance (Randrianambinina et al. 2007; Hilgartner et al. 2008). They lack sexual size dimorphism (Kappeler 1991; Ganzhorn et al. 2004) and they have evolved a number of adaptations to deal with constraints imposed by their folivorous diet despite small body size (< 1 kg). Amongst them are an enlarged cecum (Tattersall 1982), one of the lowest basal metabolic rates among folivorous mammals (Schmid and Ganzhorn 1996), extended nightly resting periods (Ganzhorn and Kappeler 1996) as well as the reingestion of feces (i.e. caecotrophy; Hladik 1978; but see Russell 1977). Although the diets of sportive lemurs have been described previously based on dietary composition and/or the nutritional value of different foods (Charles-Dominique and Hladik 1971; Nash 1998; Thalmann 2001; Ganzhorn et al. 2004; Dröscher and Kappeler 2014), the present study quantifies daily energy and nutrient intake to determine the primary nutritional goal (Felton et al. 2009a).

We aimed to explore how this small-bodied folivore living under seasonal constraints can overcome energetic constraints imposed by a diet that constitutes a poor source of readily available energy. In particular, we predicted that individuals compensate for increased energy expenditures due to thermoregulatory demands during the cold dry season by increased energy intake. In addition, we predicted that energy intake during times of gestation and lactation is higher in females than males. Moreover, we predicted that digestible protein intake in lactating females is elevated in comparison to males. Together, the answers to these questions will allow to determine which factors during which parts of the year place the greatest energetic constraints on *Lepilemur leucopus*.

Methods

Study site and species We studied a population of white-footed sportive lemurs at Berenty (S 25.00°, E 46.30°), an approximately 200 km^2 private ecotourism reserve in southern Madagascar. We observed animals in a spiny forest fragment of about 5 ha (HAH Reserve Forestière parcel 1), which is connected to gallery forest on one side via a transitional forest and a further 40 ha spiny forest fragment on the other side (Norscia and Palagi 2008). Sportive lemurs are medium-sized nocturnal folivores that forage solitarily, even when they live in pairs (Méndez-Cárdenas and Zimmermann 2009; Hilgartner et al. 2012; Dröscher and Kappeler 2013). To ensure continuing focal observations of single individuals, we equipped 20 animals with radio-tracking transmitters. For more information on animal capture see Dröscher and Kappeler (2013, 2014).

We divided the study period into four biologically relevant seasons: birth and offspring-care with lactation (early wet season from November to January), offspring-care without lactation (late wet season from February to April), mating and early gestation (early dry season from May to July) and late gestation (late dry season from August to October). We recorded minimum and maximum temperatures on a daily basis as well as the amount of precipitation after each rainfall. Seasonality in temperature and rainfall was pronounced during our study. High daytime temperatures with monthly averages of up to 35°C characterized the wet season, while monthly average nighttime temperatures fell to 15°C during the dry season. While precipitation amounted to 480mm during the wet season, we recorded only 64mm (or 12% of the annual rainfall) during the dry season (Fig. 1).

We characterized seasonal changes in food availability based on the density of food species and bimonthly phenology surveys conducted between October 2011 and October 2012 (see Dröscher & Kappeler 2013). Food availability varied seasonally.

Leaves contributed most to available food, while flowers and fruits played only a minor role. The early wet season was characterized by a dominance of young leaves. During the late wet and early dry season mature leaves dominated, while during the late dry season food availability was at its lowest.

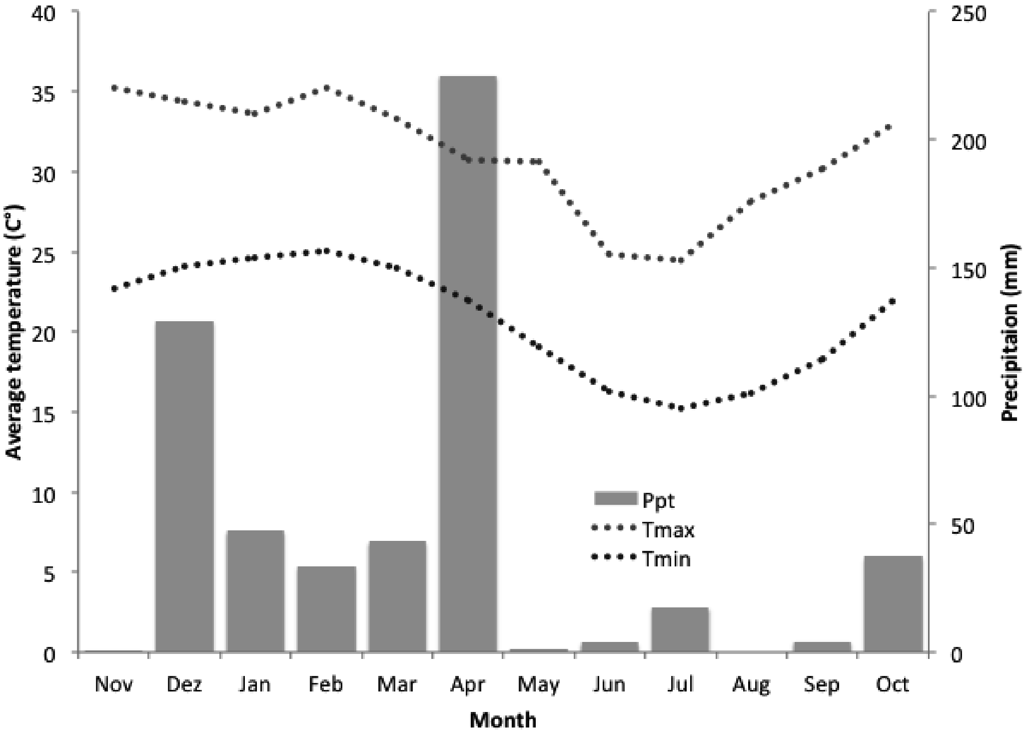

Fig. 1 Monthly average maximum and minimum temperatures (°C) as well as monthly bulk precipitation (mm) at Berenty, Madagascar, between November 2011 and October 2012.

Behavioral observations We collected behavioral data between October 2011 and October 2012 (Dröscher and Kappeler 2013, 2014). We started continuous all-night focal animal observations (Altmann 1974) when the animal left its sleeping site at dusk until it returned to its daytime sleeping site at dawn. We recorded the beginning and end of each defined behavioral state (i.e. resting, travelling, feeding and other). During each feeding bout of a focal animal, we recorded species and types of food eaten (i.e. leave, flower, fruit, shoot) along with duration of feeding on that particular food item. We distinguished between young (i.e. pale green leaves lacking a heavy cuticle), mature (i.e. deep green, structurally developed leaves) and old leaves (i.e. yellowish leaves with signs of senescence). A feeding bout started when an individual started to introduce food items into its mouth and ended when an animal stopped inserting food items for more than 15 sec. We recorded feeding rates (number of units ingested/minute) for specific food items, whenever observations conditions were favorable, to establish weight-based intake rates (g of DM/minute; Kurland and Gaulin 1987; Schülke et al. 2006; Nakagawa 2009; Rothman et al. 2012). In most cases a bite corresponded to discrete unit of food such as a leaf, a leaflet or cluster of flowers or leaves. In a few instances the quantity per bite could not be measured easily such as when eating on shoots. As mouth width and length measure approximately 2 cm, we assumed that one bite equals a piece of shoot of 2 cm length. We recorded feeding rates on 352 occasions for 35 species and 70 food items (i.e. species and food type combinations).

Food sample collection As nutrient regulation appears to occur over one day (de Castro 2000; Johnson et al. 2013) and as what an individual consumes earlier the day influences what it consumes later the day (Booth and Thibault 2000), the analyses of underlying nutritional goals requires detailed analysis of nutrient intake per individual per day and relevant nutritional analyses of all food items consumed (Felton et al. 2009a). In addition, nutrient content of plants even within a single species can vary over different spatial and temporal scales (Chapman et al. 2003; Worman and Chapman 2005). Hence, we collected food samples from all food patches the focal animals were observed to feed from during full night observations. During each of the four seasons we collected foods consumed by 6 males and 6 reproductive females, with the exception of the early wet season were we could collect foods eaten by 5 lactating females, resulting in a total of 47 full night follows for which food samples were collected. We collected the food samples on the day after the full-night observation from the exact same food patches so that the samples are representative of the nutrients in the food item ingested at that time (Rothman et al. 2012). In total we collected and analyzed 1006 food samples from 45 species comprising 98 different food items for their nutritional content. We dried samples in an oven (temperatures maintained between 45–50 °C), and later transported samples to the University of Hamburg for nutritional analyses.

Analyses of macronutrient content Samples were analyzed either via standard methods (Ortmann et al. 2006) or near infrared spectroscopy (Foley et al. 1998). Samples were ground in a Retsch-mill to a homogenous powder, analyzed in duplicates and nutrient concentrations estimated on a dry matter basis. A representative subset of samples was selected and analyzed chemically for the calibration of the spectroscope and the accuracy of the developed NIRS-models was tested using cross- and test-set-validation (Stolter et al. 2006). Neutral detergent fiber (NDF) was analyzed using an ANKOM fiber analyzer (Van Soest et al. 1991), while total nitrogen (Association of Official Analytical Chemists 1990) and ash (Rothman et al. 2012) were measured via combustion. Nitrogen digestibility was estimated in vitro using pepsin and cellulase (DeGabriel et al. 2008) to obtain a biologically more meaningful measure of protein than crude protein (Wallis et al. 2012), and fat content was determined using ether extract (Rothman et al. 2012).

Nutrient intake calculations When nutritional information for a certain food was unavailable, we substituted it with average annual or, if available, seasonal values of that particular species and food type (N = 36). Likewise, due to the arboreal nocturnal habit and the diverse diet of the study species, we were not able to record feeding rates for all food items. However, we could record feeding rates for all food species that were important in the overall diet. When feeding rates for certain food items were not available, we substituted data from other food items that most closely represented the food items in consideration in terms of shape, size and texture (N = 32). Sex and season did not affect feeding rates (GLMM: $\chi 2 = 2.788$, df = 4, P = 0.594; see below) and we averaged all recorded feeding rates for the particular food item. We multiplied feeding rates (number of units consumed/min) with the average unit dry-weight of food items (g of DM) to calculate intake rates (g of DM/minute).

We used the following formula to calculate the observed energy intake of the focal individuals during their nightly activity:

$$I = \sum_{i=1}^{n} D \times R \times E$$

where I = energy intake (kJ/total observation time), n = number of foods consumed, D = duration of feeding on particular food (min), R = intake rate (g of DM/min) and E = metabolizable energy content of food (kJ/g). We estimated the metabolizable energy content of foods by summing the energetic contributions from fat, NDF (neutral detergent fiber), TNC (total non-structural carbohydrates) and digestible protein (Rothman et al. 2012). We used energetic values of 37.7 kJ/g fat, 16.7 kJ/g digestible protein and 16.7 kJ/g TNC (National Research Council, 2003). We estimated TNC by subtracting the percentages of NDF, digestible protein, fat, and ash from 100%. We subtracted one from the percentage of ether extract to account for non-nutritive substances (Rothman et al. 2012). Information on fiber digestibility is not available for this species, so we substituted values for rabbits on the basis that like our study animals, they are small-bodied hindgut fermenters that exhibit cecotrophy and rely on an herbivorous diet. The apparent digestibility of NDF in rabbits (*Oryctolagus cuniculus* with an average body mass of 1575g) was determined as 20.8 % (Sakaguchi et al. 1987). Since anaerobic microbes keep some of the energy from fiber for themselves, only up to 3 kcal/g of fiber are available to the host (Conklin-Brittain et al. 2006). Thus the physiological fuel value is 3*0.208 = 0.624 kcal/g or 2.6 kJ/g of fiber in rabbits.

We could not determine the activity of the animals at all times, nor could we identify the food consumed on all occasions due to the animals' nocturnal activity. The animals were in sight on average 92 ± 6% of the total observation time (N = 47). The feeding time for which we could reliably identify the food consumed was on average 95 ± 8% of the total observed feeding time (N = 47). As for the purpose of the study we were interested in total daily energy intake and not in energy intake per observation time in sight, we extrapolated our data to the total activity time of the animals (i.e. from when an animal left its sleeping tree until it returned to its sleeping tree). First, we calculated the hourly energy intake (kJ/h) by dividing the observed energy intake with the total feeding time for which we could reliably identify the food consumed (h). Second, we calculated the relative feeding time (%) by multiplying the total observation time the animals was in sight (h) with 100 and a subsequent division with the total amount of time the animal was observed feeding (h). Third, we extrapolated the total daily feeding time (h) by multiplying the relative feeding time (%) with the total activity time and subsequently dividing it by 100. Finally, we calculated daily energy intake (kJ/day) by multiplying the hourly energy intake (kJ/h) with the total daily feeding time (h).

We used the geometric framework of nutrition to assess nutritional priorities and to relate observed patterns of nutrient intake with extrinsic and intrinsic factors (Simpson and Raubenheimer 1993). We consider the daily contribution of non-protein vs. protein to total daily energy intake to determine patterns of nutrient prioritization (Simpson and

Raubenheimer 1993; Raubenheimer and Simpson 1997). For the purpose of our analysis, we combined energy from fat, NDF and TNC as non-protein energy for comparison with digestible protein to investigate their relative contributions to total daily energy intake.

Data analyses We used a generalized linear mixed model (GLMM) with Poisson distribution to estimate the effect of season and sex on recorded feeding rates on leaves. We included individual identity as a random effect to control for repeated observations. In addition, we controlled for food species and food part (i.e. young, mature or old leaves). We included observation number as a random effect to account for overdispersion (Lee 2000). We calculated VIFs, dfbetas, Cook's distance and leverage running a standard generalized linear model using the function 'glm' with the random effect excluded from the predictors (Hosmer and Lemeshow 2000). Influence diagnostics indicated some problems with model stability (Quinn and Keough 2002; Field et al. 2012). However, running the model without the influential cases did not lead to a different overall result, and hence, we report the results obtained for the complete dataset.

We used linear mixed models (LMM) to estimate the effect of season and sex or temperature, respectively, on daily energy (kJ/day), digestible protein (kJ/day), non-protein (kJ/day) and food intake (g of DM/day). We included individual identity as a random effect to control for repeated observations. In addition, we controlled for the effect of individual body mass. We transformed response variables using the function 'boxcox' of the package 'MASS' (Venables and Ripley 2002) and z-transformed the covariate (Schielzeth 2010). For our linear mixed models, we checked the distribution of the model residuals, plotted residuals against predicted values, conducted the Levène's test and correlated absolute residuals with fitted values to check model validity. We visually inspected qq-plots and plots of residuals vs. fitted values. None of the diagnostics indicated obvious deviations from the assumptions of normality and homogeneity of residuals (Quinn and Keough 2002; Field et al. 2012). We calculated Variance Inflation Factors (VIFs) using the R function 'vif' of the package 'car' (Fox and Weisberg 2011) running a standard linear model with the random effect excluded from the predictors. VIFs indicated collinearity not to be an issue (Field et al 2012). For influence diagnostics (Cook's distance, dfbetas) we used the R package 'influence.ME' for mixed effect models (Nieuwenhuis et al. 2012). Influence diagnostics did not indicated problems with model stability (Quinn and Keough 2002; Field et al. 2012). To test whether sex and season, or temperature, respectively, had an overall effect on daily energy, digestible protein, non-protein or food intake, we compared the full model to a model in which only these predictors were removed (i.e. sex and season or temperature, respectively), using a likelihood ratio test. We fitted the models in R using the function 'lmer' in the package 'lme4' (Bates et al. 2012) using Maximum Likelihood rather than Restricted Maximum Likelihood to achieve more reliable P-values (Bolker et al. 2008). We derived P-values for the individual effects based on Satterthwaite approximation for denominator degrees of freedom by using the function 'summary' of the R package 'lmerTest' (Kuznetsova et al. 2014). In addition, we performed a Mann-Whitney U Test to determine sex differences in daily energy, digestible protein, non-protein and food intake as well as the non-protein to protein ratio on a season by season basis.

We used a generalized linear mixed model (GLMM) with binomial error distribution to estimate the effect of season and sex or temperature, respectively, on the ratio between non-protein and protein energy intake. We handed the response over as a matrix with two columns representing the proportions of protein and non-protein energy intake. We fitted the models in R using the function 'glmer' in the package 'lme4' (Bates et al. 2012) using a likelihood ratio test (Dobson 2002). We included individual identity as a random effect to control for repeated observations. We z-transformed the covariate (Schielzeth 2010). We calculated VIFs, dfbetas, Cook's distance and leverage running a standard generalized linear model using the function 'glm' with the random effect excluded from the predictors (Hosmer and Lemeshow 2000). Their values indicated that there were no problems with collinearity (Field et al 2012) and model stability (Quinn and Keough 2002; Field et al. 2012).

We tested for sex differences in activity budgets on a season by season basis using Welch's unequal variance t-test. We restricted our analyses of activity budgets to 7 males and 6 reproductive females which we could follow repeatedly twice per season across all four seasons (N = 104 observations nights). For the analyses, we averaged nightly values for each season (N = 52 based on four seasons and 13 individuals). We based estimates of activity budgets (resting, feeding, and traveling) on the time the animals were in sight. We considered alpha levels of $P \leq 0.05$ as statistically significant.

Results

Seasonality in food content Macronutrient concentration and energy density of important food items were similar across all four seasons (Table 1). Concentrations of digestible protein (ANOVA: F(1, 91) = 1.375, P = 0.247), TNC (F = 1.538, P = 0.218), NDF (F = 1.23, P = 0.270) and fat (F = 3.689, P = 0.058) did not differ significantly between seasons. Similarly, digestible protein (F = 1.495, P = 0.225), non-protein (F = 2.927, P = 0.091) as well as total energy content (F = 0.853, P = 0.358) showed no significant seasonal variation.

Table 1 Seasonality in macronutrient concentration (%) and energy density (kJ/g) of important food items (i.e. contributing >1% of feeding time) of *Lepilemur leucopus* in the spiny forest at Berenty, Madagascar. Percentage values represent percentage of dry matter (cP = crude protein, dP = digestible protein, TNC = total non-structural carbohydrates, NDF = neutral detergent fiber, non-P = non-protein, P = protein).

Nutrient content	Early wet season (N = 27)	Late wet season (N = 26)	Early dry season (N = 19)	Late dry season (N = 21)
cP (%)	16.9±6.5	16.3±4.9	15.5±3.4	15.4±4.9
dP (%)	12.4±6.4	11.6±4.6	10.4±3.6	11.0±5.3
TNC (%)	41.1±8.5	36.9±8.5	43.0±6.5	42.5±8.2
NDF (%)	33.8±10.4	38.1±9.8	31.8±7.9	32.3±9.6
Fat (%)	1.6±0.9	2.2±1.4	2.7±1.6	2.2±1.5
Non-P (kJ/g)	8.3±1.4	8.0±1.3	9.0±1.4	8.8±1.6
P (kJ/g)	2.1±1.1	1.9±0.8	1.7±0.6	1.8±0.9
Total (kJ/g)	10.4±1.5	9.9±1.4	10.8±1.5	10.6±1.7

Food nutritional composition Food types differed in their macronutrient compositions (Table 2). Leaves were the main contributors to the diet of *L. leucopus*. Concentrations of digestible protein (Kruskal-Wallis test: $\chi2$ = 105.899, df = 2, P < 0.001), fat ($\chi2$ = 101.534, df = 2, P < 0.001), TNC ($\chi2$ = 58.514, df = 2, P= < 0.001) as well as digestible protein energy ($\chi2$=96.967, df = 2, P < 0.001) and non-protein energy content ($\chi2$ = 75.506, df = 2, P < 0.001) differed significantly across leave maturity stages. However, neutral detergent fiber (Kruskal-Wallis test: $\chi2$ = 5.351, df = 2, P = 0.069) and total energy content was similar across young, mature and old leaves ($\chi2$ = 3.394, df = 2, P = 0.183). Digestible protein concentrations were highest in young and lowest in old leaves (Wilcoxon rank sum test with Bonferroni correction: P < 0.001). In contrast, TNC concentrations as well as non-protein energy were highest in old and lowest in young leaves ($P \leq 0.0037$).

Table 2 Macronutrient concentration (%) and energy density (kJ/g) of foods eaten by *Lepilemur leucopus* in the spiny forest at Berenty, Madagascar. Percentage values represent percentage of dry matter (dP = digestible Protein, TNC = total non-structural carbohydrates, NDF = neutral detergent fiber, non-P = non-Protein, P = Protein).

Plant part	N	dP (%)	TNC (%)	NDF (%)	Fat (%)	Non-P (kJ/g)	P (kJ/g)	Total (kJ/g)
YL	235	13.8±6.7	34.2±11.7	40.6±15.8	1.0±1.3	7.1±1.9	2.3±1.1	9.4±2.4
ML	483	9.8±4.8	38.3±9.2	38.2±12.1	1.9±1.7	8.1±1.7	1.6±0.8	9.7±1.9
OL	229	8.1±4.2	40.9±6.2	37.1±8.9	1.8±1.1	8.5±1.0	1.4±0.7	9.8±1.2
Shoot	33	12.6±7.3	38.1±8.3	33.0±12.1	2.3±1.4	8.1±1.2	2.1±1.2	10.2±1.2
Flowers	23	9.5±5.7	45.8±8.0	35.9±7.2	2.1±1.3	9.4±1.1	1.6±1.0	11.0±1.2
Fruits	3	7.8±0.5	38.0±7.4	44.7±5.8	3.2±1.3	8.7±1.1	1.3±0.1	10.0±1.0

Effect of sex and season on daily intakes The average daily dry matter intake of the study animals was 63 ± 14 g/day and the average daily energy intake was 602 ± 153 kJ/day (N = 47; Fig. 2a). Energy intake was 874 kJ/kg$^{0.762}$ and digestible protein intake was 156 kJ/kg$^{0.762}$ metabolic body mass per day. Across the study period, the animals maintained an average daily intake of 4.8 ± 1.28 kJ non-protein to protein energy balance, with the ratio ranging between 2.63 and 7.97. The full model comprising the effects of sex and season was significant as compared to the null model with respect to total energy intake (LMM; likelihood ratio test: $\chi 2 = 16.543$, df = 4, P = 0.002), non-protein energy intake ($\chi 2 = 17.984$, df = 4, P = 0.001) and food intake ($\chi 2 = 12.666$, df = 4, P = 0.013) as well as the ratio of non-protein to protein energy intake (GLMM; $\chi 2 = 68.674$, df = 4, $P < 0.001$). More specifically, season, but not sex, had an overall significant effect on total energy, non-protein, and food intake (Table 3) as well as the ratio of non-protein to protein energy intake (Table 4; Fig. 2b). However, the full model was not significant compared to the null model with respect to total digestible protein intake ($\chi 2 = 1.641$, df = 4, P = 0.801). Also on a season by season basis sexes did not differ significantly in any of the explored intake variables (Mann-Whitney U-test: $W < 26$, $P > 0.240$; Table 5).

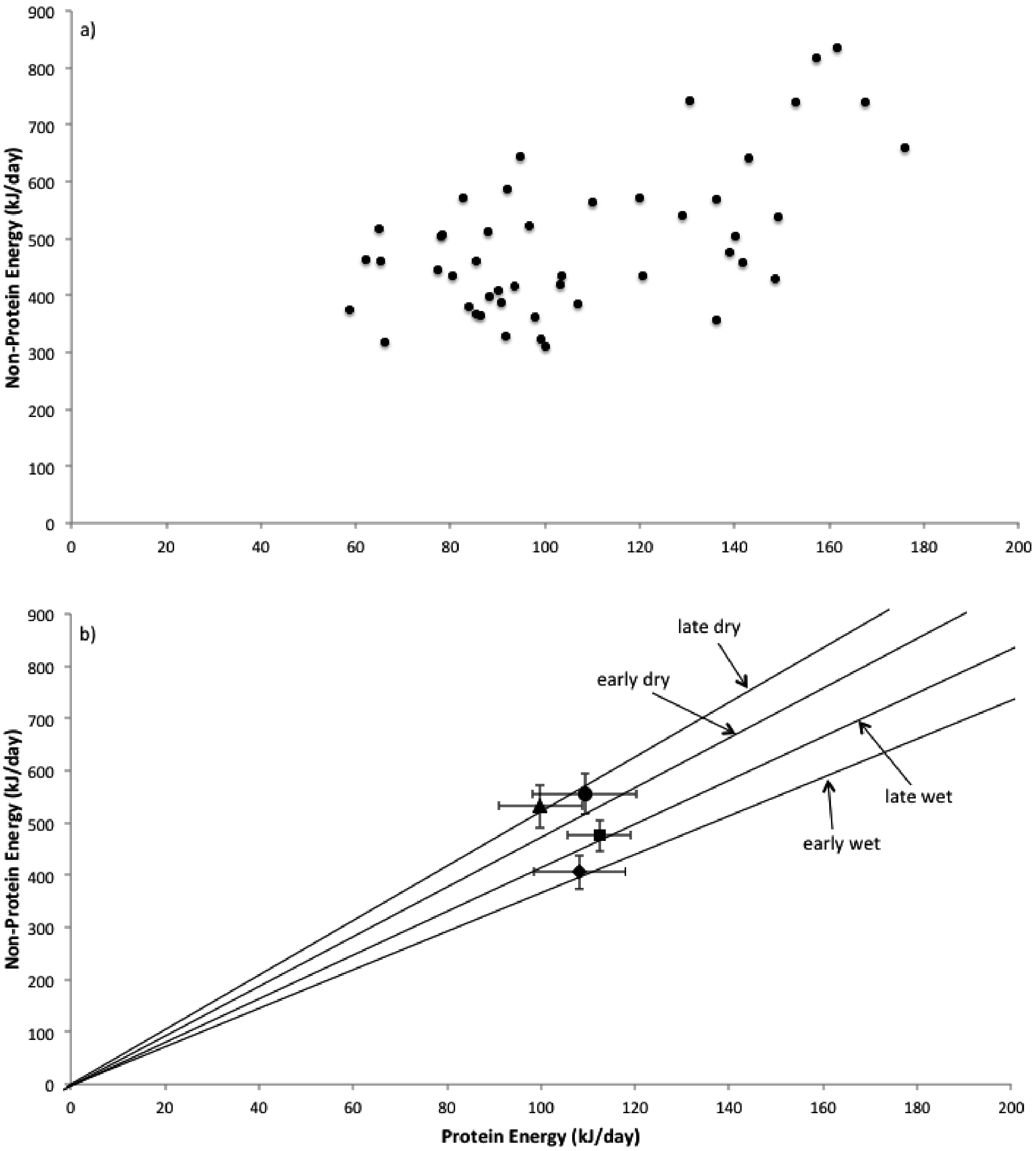

Fig. 2 Intake of protein and non- protein energy by *Lepilemur leucopus* in the spiny forest at Berenty, Madagascar. **(a)** Daily intakes based on 47 full night continuous focal observations conducted between November 2011 and October 2012. **(b)** Plot of mean daily intakes (±S.E.) during the early wet (diamond), late wet (square), early dry (triangle) and late dry season (circle). Lines radiating from the origin represent nutritional rails and indicate the digestible protein and non- protein energy balance in the four seasons.

Table 3 Effects of sex (males N = 24, females N = 23), season and body mass on daily intakes (LMM). Significant effects are indicated in bold.

Fixed Factor	β	SE	df	t	P
Total Energy (kJ/day)					
Intercept	7.782e-04	3.427e-04	10.35	2.271	0.046
Sex (male)	-9.816e-06	5.082e-05	9.733	-0.193	0.851
Late wet	-9.342e-05	3.379e-05	11.39	-2.765	**0.018**
Early dry	-1.224e-04	3.390e-05	11.43	-3.609	**0.004**
Late dry	-1.509e-04	3.431e-05	11.60	-4.397	**0.001**
Body mass	-4.405e-07	5.391e-07	10.38	-0.817	0.432
Non-Protein Energy (kJ/day)					
Intercept	3.952e-03	1.533e-03	12.28	2.578	0.024
Sex (male)	-2.418e-05	2.254e-04	10.85	-0.107	0.917
Late wet	-4.777e-04	1.739e-04	25.11	-2.746	**0.011**
Early dry	-6.913e-04	1.744e-04	25.23	-3.963	**0.001**
Late dry	-7.991e-04	1.762e-04	25.89	-4.536	**0.000**
Body mass	-1.840e-06	2.413e-06	12.35	-0.763	0.460
Food intake (g of DM/day)					
Intercept	1.438e-02	5.920e-03	12.31	2.430	0.031
Sex (male)	-2.363e-04	8.789e-04	11.25	-0.269	0.793
Late wet	-1.002e-03	5.733e-04	29.20	-1.747	0.091
Early dry	-1.432e-03	5.733e-04	29.36	-2.489	**0.019**
Late dry	-2.219e-03	5.824e-04	30.00	-3.810	**0.001**
Body mass	-8.719e-06	9.314e-06	12.37	-0.936	0.367

Table 4 Effects of sex (males N = 24, females N = 23) and season on the ratio of non-protein to protein energy intake (GLMM). Significant effects are indicated in bold.

Fixed Factor	β	SE	z	P
Intercept	1.353	0.050	27.232	<0.001
Sex (male)	-0.039	0.055	-0.708	0.479
Late wet	0.123	0.046	2.679	**0.007**
Early dry	0.347	0.047	7.445	**<0.001**
Late dry	0.293	0.047	6.307	**<0.001**

Table 5 The results of the Mann-Whitney U-test for sex-specific differences in daily energy and food intake on a season by season basis (1 = early wet season; 2 = late wet season; 3 = early dry season; 4 = late dry season). Values given for males and females are means and standard deviations.

Variable	Season	Male	Female	W	P
Total Energy (kJ/day)	1	527±157	528±99	22	0.247
	2	604±89	617±156	14	0.575
	3	667±170	640±149	16	0.818
	4	674±164	707±135	21	0.699
Non-Protein (kJ/day)	1	400±132	414±82	21	0.329
	2	462±43	489±82	16	0.873
	3	542±158	522±140	17	0.937
	4	539±140	572±138	21	0.688
Protein (kJ/day)	1	103±38	114±27	20	0.429
	2	118±25	106±22	13	0.485
	3	103±30	96±34	13	0.485
	4	108±45	110±38	21	0.748
Non-Protein : Protein	1	4.0±0.7	3.7±0.7	12	0.662
	2	4.0±0.9	4.6±0.8	26	0.240
	3	5.2±0.4	5.6±1.1	20	0.818
	4	5.6±2.1	5.5±1.4	17	0.937
Food intake (g of DM/day)	1	59±20	56±9	21	0.311
	2	61±9	60±15	14	0.475
	3	65±17	62±15	16	0.818
	4	67±15	72±14	21	0.699

Effect of temperature on daily intakes The full model comprising the effect of temperature was significant as compared to the null model with respect to total energy (LMM; $\chi2 = 8.215$, df = 1, $P = 0.004$), non-protein energy ($\chi2 = 10.925$, df = 1, $P < 0.001$) and food intake ($\chi2 = 5.139$, df = 1, $P = 0.024$) as well as the ratio of non-protein to protein energy intake (GLMM; $\chi2 = 7.441$, df = 1, $P < 0.001$). However, the full model was not significant compared to the null model with respect to total digestible protein intake ($\chi2 = 1.391$, df = 1, $P = 0.237$). More precisely, total energy (one-tailed Spearman rank correlation: N = 47, $r_s = -0.343$, $P = 0.009$), non-protein energy ($r_s = -0.413$, $P = 0.002$) and the ratio of non-protein to protein energy intake ($r_s = -0.511$, $P < 0.001$) as well as food intake ($r_s = -0.264$, $P = 0.036$) were negatively related to temperature.

Sex difference in activity patterns The amount of time spent travelling differed significantly between the sexes during the early wet (Welch two-sample t-test: t = -4.078, df = 8.741, P = 0.003), but not during the late wet (t = -1.763, df = 8.584, P = 0.113), early dry (t = 0.406, df = 10.961, P = 0.693) and late dry season (t = -1.497, df = 9.887, P = 0.166). In particular, males (mean ± SD: 8.25 ± 1.86 % of observation time) spent more time travelling during the early wet season than females (5.04 ± 0.86 %). In contrast, the amount of time spent resting (Welch two-sample t-test: $t \geq -0.693$, $df \leq 10.715$, $P \geq 0.503$) or eating ($t \leq 0.8186$, $df \leq 10.454$, $P \geq 0.431$) did not differ between sexes, regardless of season.

Discussion

We tested whether changing reproductive state and varying environmental conditions are reflected in corresponding changes in individuals' nutritional goals. We found that *L. leucopus* balanced their nutrient intake. While they maintained a stable daily digestible protein intake across seasons and reproductive stages, they increased daily non-protein energy intake with decreasing ambient temperatures through active food selection and an increase in food intake. Contrary to our predictions, males and females did not differ in their nutrient or energy intake regardless of female reproductive state, nor did lactating females increase their digestible protein intake.

Effects of Seasonality on Energy and Protein Intake Behavioral and physiological changes often parallel annual changes in environmental conditions such as climate and food availability (Morland 1993). While diurnal species seem to be seasonally more affected by heat stress as indicated by shifts in activity periods and increased resting time (Hill 2006; Ossi and Kamilar 2006; Bourgoin et al. 2008; Campos and Fedigan 2009;

Shrestha et al. 2014), nocturnal species may be affected seasonally by cold temperatures during their periods of activity (Schmid and Kappeler 2005). *Lepilemur* spp. increase resting time during the cold dry season (Nash 1998; Dröscher and Kappeler 2014), and we demonstrated an increase in daily energy intake. The most extreme adaptations to cope with seasonal food shortages and low temperatures are daily torpor and hibernation (Geiser 1998; Schmid and Speakman 2000). For example, *Microcebus griseorufus* (reddish-grey mouse lemur), which also inhabit the spiny forests of Southern Madagascar, engage in torpor and/or hibernation during the cold dry season (Génin 2008; Kobbe and Dausmann 2009). While the spiny forests are a highly unpredictable environment regarding amount and distribution of annual rainfall (Gould et al. 1999; Jolly et al. 2002; Génin 2008), folivorous *L. leucopus* do not seem to be constrained by food availability during the cold dry season, at least during years of average or better rainfall (Dröscher and Kappeler 2014), but rather by low temperatures due to thermoregulatory demands, as indicated by an increase in daily energy intake with decreasing ambient temperatures. Additional studies linking seasonality in daily energy intakes with seasonal energy expenditures would further our knowledge about the extent by which heightened energy demands for thermoregulation can be met by increased energy intake.

At low temperatures, food intake can be expected to be higher for heat production to counteract hypothermia (Brobeck et al. 1943, Goymann et al. 2006) and *L. leucopus* met its seasonally increased energy demand by a seasonal increase in food intake. *Lepilemur leucopus* increased daily food intake with decreasing nightly minimum temperatures during the cold dry season, even though food availability reached a minimum during the late dry season. Similarly, *Varecia variegata* (black-and-white ruffed lemurs) increased feeding during the months with lowest temperatures (Morland 1993); however, no information is available how this effect translates in seasonal differences in energy intake. One possibility is that gut capacity itself may change when mammals are faced with increased energy requirements during exposure to cold temperatures to accommodate a greater need for food processing (Gross et al. 1985; Toloza et al. 1991; Foley and Cork 1992; Ganzhorn et al. 2003). It remains an open question, however, which behavioral and physiological mechanisms are available to *L. leucopus* and other lemurs to deal with food shortage during drought years when they may not be able to reach the required energy intake imposed by thermoregulatory demands.

Lepilemur leucopus does not seasonally shift its diet, and leaves of the most abundant tree species dominate the diet regardless of season (Dröscher and Kappeler 2014). While folivorous *L. leucopus* could increase food and, hence, total energy intake during the cold dry season, a different pattern characterizes frugivorous-folivorous *Propithecus diadema* (diademed sifaka). During the dry season, *P. diadema* shifted from a fruit dominated diet to a diet based on leaves and flowers. At the same time it dramatically reduced daily food and energy intake, probably due to greater postingestive processing challenges of the more folivorous diet (Irwin et al. 2014). Relatively folivorous species are generally less susceptible than more frugivorous species to forest degradation (Irwin and Raharison 2009), hurricane events (Pavelka et al. 2003) and climate change (Wiederholt and Post 2010; reviewed in Schwitzer et al. 2011). Taken together, these observations indicate that species that rely more on fruits may be more susceptible to unpredictability in climate and food availability than species that subsist on a leaf-based diet.

Ambient temperature can be expected do have an influence not only on total food/energy intake but also on food selection. While daily intake of digestible protein did not differ across seasons, daily intake of non-protein energy varied seasonally and, more particularly, increased with decreasing temperatures. This pattern resulted in a seasonally variable ratio of non-protein to protein energy, which also increased with decreasing temperatures. Similarly, experimental studies found that animals increase their carbohydrate/fat consumption but not their protein intake with decreasing ambient temperatures (Donhoffer and Vonotzky 1947; Aubert et al. 1995). The average composition of the most used food items did not vary across seasons in terms of macronutrient and energy content (see also Irwin et al. 2014), indicating that *L. leucopus* reached the seasonally increase ratio of non-protein to protein energy through active food selection. Our findings suggest that ambient temperature conditions should be given greater consideration in future studies on food selection and nutritional ecology, especially if the study species lives in a habitat with marked seasonal fluctuations in ambient temperatures.

Nutritional goals may differ across species according to the nutritional quality of their foods. *Lepilemur leucopus* maintained a stable daily digestible protein intake across seasons, prioritizing protein in relation to non-protein energy. This matches the findings for *Ateles chamek* (Peruvian spider monkey; Felton et al. 2009b). In contrast, *Gorilla beringei* (eastern gorilla) prioritize non-protein energy and over-ingest protein when eating a leaf-based diet, rather than targeting leaves to supplement a protein-limited diet (Rothman et al. 2011). Owing to the low protein content of fruit pulp, frugivorous primates have diets of relatively low protein content, while most folivorous primates have diets high in protein since leaves contain considerable quantities of rubisco, a protein involved in photosynthesis (Oftedal et al. 1991; Curtis 2004; Simmen et al. 2007). For example, *G. beringei* eat diets where the ratio of protein to energy is similar to the maximum recommended protein intake for humans (Rothman et al. 2011) and *Procolobus rufomitratus* (red colobus monkey) in Uganda eat leaves that contain up to 40% crude protein (Ryan et al. 2013). In general, higher metabolic rates in small animals lead to higher rates of protein requirements per unit body mass compared to larger mammals (Mattson 1980). With digestible protein concentrations of their natural food at about 11%, *L. leucopus* might have difficulty meeting protein requirements. For example, the distribution of *Lepilemur ruficaudatus* (red-tailed sportive lemur) is closely related to protein availability during the wet season (Ganzhorn 2002). Similarly, a number of folivorous marsupials are limited by the low protein content of *Eucalyptus* foliage (DeGabriel 1983; Foley and Hume 1987; Kavanagh and Lambert 1990; DeGabriel et al. 2009). While foregut fermenters can meet parts of their protein requirements by digesting microorganisms from the forestomach, microbial protein is not directly available to hindgut fermenters (Parra 1978; Foley and Cork 1992). However, in many small herbivorous mammal species with hindgut fermentation a higher rate of nitrogen utilization is achieved by means of cecotrophy (Hirakawa 2001; Sakaguchi 2003), an adaptation that has also been described in *L. leucopus* (Hladik 1978).

Effects of Reproduction on Energy and Protein Intake Males and females of *L. leucopus* did not differ in any of the nutritional variables measured (i.e. total energy, non-protein and digestible protein intake and the ratio of non-protein to protein intake). Similarly, while the amount of food ingested or the relative contribution of various items to food composition were not considered, males and females of the congener *L. ruficaudatus* were shown to select food of similar chemical composition during the wet season (time of lactation and weaning), indicating that females do not compensate the costs of lactation by improving food quality (Ganzhorn et al. 2004). While sexes may differ in their digestive efficiency to compensate for differing reproductive investment (Ganzhorn et al. 2004), resting (Schmid and Ganzhorn 1996) and field metabolic rates (Drack et al. 1999) of *L. ruficaudatus* did not differ between sexes, indicating that males and females may simply not differ in their energetic requirements. The measurements were restricted temporarily to the time of early gestation (Drack et al. 1999) and to post-weaning/pre-mating and mid to late gestation, respectively (Schmid and Ganzhorn 1996). Similarly, total energy expenditures were shown to not differ between sexes in *Lemur catta* (ring-tailed lemur) and *Eulemur sp.* (brown lemur; Simmen et al. 2010). To examine in more detail whether energetic costs of reproduction differ among males and females in *L. leucopus*, measurements on daily energy expenditures during the lactation period would be insightful.

In general, females could compensate their energetic requirements associated with birth and lactation by reduced locomotion compared to males (Ganzhorn et al. 2004). Males of *L. leucopus* spent more time travelling during the early wet season than females. Similarly, male *L. ruficaudatus* traveled longer distances per night than females during the wet season (Pietsch 1998). Likewise, in monomorphic *Tamiasciurus hudsonicus* (red squirrel) energetic costs of males approximate those of females due to male locomotory costs linked to mate searching efforts (Lane et al. 2010). In contrast, *L. leucopus* lives in pairs and, hence, mate searching can be considered a minimal cost. Instead, increased male travelling during birth and lactation indicates that energetic costs of male investment in reproduction may be instead related to protective behavior to ward off potentially infanticidal males (Gubernick 1994; Palombit 1999; Borries et al. 2010). While the benefits to males from infanticide in sportive lemurs are not known as they breed strictly seasonally, infanticide poses a real thread. Infanticide was observed in *L. edwardsi* (Milne-Edwards' sportive lemur), where a male newcomer killed the infant of a female whose male partner had left (Rasoloharijaona et al. 2000). Similarly, we observed one case of infanticide by a male *L. leucopus* that took over the territory after death of the resident male. Thus, even in species without direct paternal care, reproductive investment may be similar in males and females.

While females are assumed to experience a peak in energetic costs during lactation (Portman 1970), average daily energy intake was lowest during the lactation period in *L. leucopus*. This indicates that thermoregulation may be more costly than reproduction for *L. leucopus*. Similarly, energy requirements and food intake are greater in both lactating and non-lactating females of *Phascolarctos cinereus* (koala) in winter than summer, presumably due to demands of thermoregulation (Krockenberger 2003). Sportive lemurs, like many nocturnal primates, are infant parkers (Rasoloharijaona et al. 2000; Hilgartner et al. 2008) and infant parking eliminates the need to constantly carry offspring, reducing energetic constraints on females (Tecot et al. 2012) as well as behavioral costs regarding foraging efficiency and predator avoidance (Schradin and Anzenberger 2001). As female *L. leucopus* are able to travel and forage unhampered, they should theoretically be able to obtain a higher average daily energy intake than observed and, thus, it appears that requirements were met. In most lemur species offspring is born and weaned during periods of food abundance (Rasmussen 1985; Sauther 1998; Vasey 2002) and seasonality in reproduction is seen as an adaptation of females to compensate for peaks in energy expenditure (Sadleir 1969, Janson and Verdolin 2005). In *L. leucopus* breeding seasonality may be rather associated with assuring adequate ambient temperatures for the altricial newborn offspring that may be limited in their thermoregulatory capacities (Tecot et al. 2012; Hull 1973) as well as sufficient nutritional intake for independent offspring (Wright 1999; Tecot et al. 2012). Females of *Avahi* spp. (woolly lemur), a genus that occupies a similar ecological niche as *Lepilemur* spp., carry their infants during the active period (Thalmann 2001), and comparative studies would further our understanding of the energetic costs of differing styles of maternal care.

Contrary to our predictions, digestible protein intake was not increased in females during the lactation period in *L. leucopus*. In general, high-protein foods are considered critical for milk production and young leaves are the most easily digested source of plant protein (Vasey 2002). The lactation period of *L. leucopus* was characterized by a dominance of young leaves, which were higher in digestible protein content compared to mature and old leaves. Hence, it seems unlikely that females were constrained in their ability to acquire higher protein intakes during the early wet season. Instead, it seems that higher dietary protein levels were not required, maybe because leaves constitute foods of balanced amino acid composition (Oftedal et al. 1991). In addition, the ratio of non-protein to protein intake was lowest during the early wet season, resulting in a diet with higher proportional protein content than during other times of the year. The balance between non-protein and protein energy intake may be of greater importance than absolute intakes (Johnson et al. 2013).

Energetic constraints imposed by a folivorous diet The average daily energy intake of *L. leucopus* was 602 ± 153 kJ/day. No direct measurements on daily energy expenditures are available for *L. leucopus*, however, resting and field metabolic rates were determined previously for the congener *L. ruficaudatus* (Schmid and Ganzhorn 1996; Drack et al. 1999). Field metabolic rates in *L. ruficaudatus* averaged 509 ± 215 kJ/day based on measurements of adult individuals (Drack et al. 1999). Sportive lemurs seem to be able to meet their energy requirements, despite their subsistence on a lower-than-expected quality diet with regard to their body size. Similarly, *Alouatta caraya* (black howler monkeys), commonly assumed to be energy-limited due to their leaf-dominated diet, are able to meet their estimated energy requirements (Amato and Garber 2014). Additional measurements of field metabolic rates in *Lepilemur* spp. specifically and folivorous primates in general would provide more insight on seasonal, species- and habitat-specific energy requirements.

The average daily food intake in *L. leucopus* was 63 ± 14 g of dry matter and equaled a dry matter intake of 10 ± 2 % of their body mass. Among primates, a similar high dry matter intake (10% of body mass) has been observed in *Cercopithecus talapoin* (Clauss et al. 2008). *Lepilemur leucopus* is a cecum fermenter (Chivers and Hladik 1980) and comparing cecum, colon, non-ruminant and ruminant foregut fermenters among mammalian herbivores, high dry matter intakes are commonly found among cecum fermenters, with the highest dry matter intake recorded in *Microtus ochrogaster* (Prairie vole, 20%; Clauss et al. 2007). Based on interspecific comparison, higher intakes are correlated with shorter mean retention time of ingesta (Clauss et al. 2007), allowing an increase in the total amount of food that can be processed (Chapman et al. 2012).

The structure of the hindgut of *Lepilemur* allows for selective retention of solutes and finer particles, while larger particles of dietary fiber are more rapidly excreted (Cork 1994; Nash 1998). The separation of the digesta occurs in the proximal colon, and solutes and fine particles and microorganisms are retained in the cecum (Foley and Cork 1992). This digestive strategy is also found in *Phascolarctos cinereus* (koala; Cork and Warner 1983) and *Brachyteles arachnoids* (woolly spider monkey; Garber 1987). In general, primate digestive strategies occur along a continuum from an “efficiency” (low intake, long mean retention time, high fiber digestibility) to an “intake” (high intake, short mean retention time, low fiber digestibility) strategy (Clauss et al. 2008). It seems that *L. leucopus* follows an “intake” strategy to meet energy requirements despite a low-quality diet and physiological constraints imposed by small body size. Information on differential gut transit time of fine soluble and large fibrous particles in *Lepilemur* would advance our knowledge of adaptations to a low-quality diet in small-bodied folivores.

GENERAL DISCUSSION

The aim of this concluding chapter is to provide a synopsis of the key findings from the earlier chapters, to discuss them in a broader perspective and to outline some approaches for future studies that could fill gaps in our current understanding of diet-related adaptations and constraints of folivores.

Synopsis of key findings

To investigate the types and consequences of feeding competition within and between social units of the solitarily foraging folivorous *Lepilemur leucopus* (white-footed sportive lemur), I first had to identify the natural social unit of this species and to describe patterns of social interactions (Chapter 1). I could show that the basic social unit consists of one adult male and female and their associated offspring. At the same time, males and females sharing a home range were characterized by low spatial cohesiveness, including signs of active avoidance, as well as very low rates of direct social interactions. Congruently, pair partners never shared their sleeping trees and never engaged in allogrooming.

Based on the rather unusual social system of *L. leucopus*, I set out to explore whether the active avoidance between pair-partners is a consequence of competition for food (Chapter 2). I could not find evidence for feeding competition in *L. leucopus*, which is most likely explained by the low selectivity in dietary choice and the primarily use of the most abundant plant species. Predation pressure at the study site was relatively high and I concluded that an anti-predator strategy based on solitariness and crypsis may be a better predictor of spatial avoidance between pair-partners than competition for food.

Although it has been suggested previously that latrine use in sportive lemurs may be linked to resources defense such as of important food patches, I tested this hypothesis empirically (Chapter 3). Communal use of latrines in *L. leucopus* rejects the idea that they are used to signal resource use among members of a social unit. In addition, *L. leucopus* did not preferentially mark food trees nor was individual feeding effort greater within than outside the latrine area, indicating that latrines are not used to signal to other social units the willingness to defend ones food resources. These results are in line with the observation that *L. leucopus* rely on the most common food species and rarely engage in conflict over food neither within nor between social units (Chapter 2). Instead, my observations support the hypothesis that latrine use functions in the maintenance of social bonds between members of a social unit.

As rates of competition were not increased during the lean season, *L. leucopus* seems to be more constrained by food quality than quantity (Chapter 2). I investigated how seasonal changes in food quantity, quality and ambient temperature influence behavior and nutrient intake in *L. leucopus*. I found that nocturnal *L. leucopus* seems to be seasonally affected by cold temperatures based on seasonal changes in activity patterns (Chapter 2). However, *L. leucopus* could increase daily food and energy intake during the cold dry season to meet thermoregulatory demands (Chapter 4). In contrast, *L. leucopus* maintained a stable daily protein intake across seasons, prioritizing protein in relation to non-protein energy, indicating that dietary protein may be in limited supply.

I studied sex-specific nutrient intake across seasons and reproductive stages (Chapter 4). I found that males and females of *L. leucopus* did not differ in energy or protein intake irrespective of female reproductive stage. The energetic costs of males approximate those of lactating females due to male locomotor costs. As average daily energy intake was lowest during the lactation period, I concluded that thermoregulation may be more costly than reproduction for *L. leucopus*. Similarly, daily protein intake was not elevated during the lactating season. However, the ratio of non-protein to protein intake was lowest during the early wet season, resulting in a diet with higher proportional protein content than during other times of the year.

I explored how *L. leucopus,* can cope with a diet that can be considered deviant for the given body size (Chapter 4). By comparing daily energy intake of *L. leucopus* with field metabolic rates previously measured in a congener (*L. ruficaudatus*), I found that animals seem to be able to meet their energy requirements. In addition, individual daily dry matter intake was high, indicating that *L. leucopus* follow an intake strategy opposed to an efficiency strategy to meet their energy requirement to overcome dietary constraints imposed by their folivorous diet despite small body size.

How does the distribution and abundance of food resources influence feeding competition and social relationships in solitary foragers?

The socio-ecological model describes the distribution of risks and resources in the environment as the main ecological factors shaping individual behavioral interactions (Jarman 1974; Terborgh and Janson 1986; van Schaik 1989) and identifying the relative importance of these bottom-up and top-down processes for the evolution and maintenance of social systems is a primary objective of behavioral ecology (Dammhahn and Kappeler 2010). The observed intersexual avoidance between pair-partners of folivorous *L. leucopus* (Chapter 1) cannot be explained by avoidance of competition over food resources, as conflicts over food resources were rarely observed, and inter-individual avoidance did not increase when food availability was low (Chapter 2). In contrast, in insectivorous *Tarsius spectrum* (spectral tarsiers) intragroup encounters decrease in frequency during the dry season (Gursky 2000) and in gummivorous *Phaner pallescens* (pale fork-marked lemurs) low cohesiveness between pair-partners results from avoidance of direct feeding competition (Schülke and Kappeler 2003). Likewise, frugivorous *Pongo pygmaeus* (Bornean orangutans) live solitary lifestyles primarily because of poor food density (Delgado and van Schaik 2000).

In general, social living co-evolved with a shift from a nocturnal to a diurnal lifestyle, supporting the role of predation in driving social evolution in primates (Shultz et al. 2011). Anti-predator strategies available to diurnal social primates may not be available to nocturnal animals, making solitariness and crypsis viable alternative strategies (Terborgh and Janson 1986). Correspondingly, sportive lemurs do not rely on early warning of predators, but direct alarm calls toward the predator (Fichtel 2007). These findings indicate that the social relationships in sportive lemurs may be mostly shaped by top-down processes. Similarly, diurnal *Cynictis penicillata* (yellow mongooses) remain solitary foragers even though their diet does not place constraints on group foraging (Nel and Kok 1999), as crypsis is an important part of the anti-predator behavior of *C. penicillata* (Roux et al. 2009). Hence, the relative contribution of bottom-up processes in shaping social systems of solitary foragers seems to be determined by species-specific diets and resource characteristics such as contestability.

Although an anti-predator strategy based on crypsis may explain at least partly female-female avoidance in sportive lemurs, also resource competition may reduce the potential for female association (Dammhahn and Kappeler 2009). Proximate mechanisms of feeding competition should be tested in relation to individuals' energy gain and reproductive success to be able to make explicit predictions about female social relationships (Janson 1988; Koenig 2002). For example, strong within-group contest and scramble competition resulted in a negative family-size effect on female net energy gain and fertility in *Phaner pallescens* (Schülke 2003). To examine whether scramble competition for food reduces the potential for female association in sportive lemurs, further studies on the effects of family size, territory size and territory quality on female reproductive success are required.

How does seasonal variation in food quantity and quality as well as ambient temperature influence activity patterns and food choice?

Fallback foods are often abundant and widely available but may be challenging to access and/or digest (Marshall and Wrangham 2007; Vogel et al. 2009). For example, *Propithecus diadema* (diademed sifakas) exhibit a dramatic decrease in food intake, likely due to greater postingestive processing challenges of the more folivorous lean season diet rather than due to limited availability of its fallback food (Irwin et al. 2014). In contrast, foods chosen, dietary diversity (Chapter 2) and the average nutritional composition of the chosen foods (Chapter 4) did not change distinctly from the wet to the dry season in *L. leucopus*. In addition, *L. leucopus* could increase food intake during the dry season despite a decline in food availability (Chapter 4). These findings indicate that *L. leucopus* are not affected by food quantity, possibly due to their folivorous diet and the inclusion of the most abundant plant species in their diet. As *Avahi* spp. (woolly lemurs) are similar to sportive lemurs in terms of nocturnality, degree of folivory and body mass, but do not base their dietary choice on food abundance (Thalmann 2001; Norscia et al. 2012), comparative studies would further our understanding of the adaptations to seasonality in folivores.

Although many primate studies have investigated seasonal variation in diet composition (Hemingway and Bynum 2005), less is known about seasonality in macronutrient intake (Irwin et al. 2014). *Lepilemur leucopus* maintained a stable daily protein intake across seasons, prioritizing protein in relation to non-protein energy

(Chapter 4). Animals require protein for growth, maintenance, reproduction, homeostasis and immune function (Lee et al. 2008; Leonard 2000; Sare et al. 2005). Because protein requirements per unit of body mass tend to increase with decreasing body mass (Lehman 2007), small folivores may be more constrained by low protein concentrations in leaves than larger primates (Norscia et al. 2012). A fundamental issue in ecology is the identification of factors that affect animal density and distribution over space and time (Gogarten et al. 2012) and protein availability has been suggested to be a major limiting factor for primate abundance (Chapman et al. 2004; Ganzhorn et al. 2009). Estimates of population density of *L. leucopus* at Berenty are much higher for the gallery (810 individuals/km^2) than for the spiny forest (200–350 individuals/km^2; Charles-Dominique and Hladik 1971; Hladik and Charles-Dominique 1974). As these two forest habitats do not differ in regional climatic conditions, but differ fundamentally in plant community composition, a comparative study may provide valuable insight into the effects of food quality on the abundance of small-bodied folivores.

Although the tropical climates in which most primate species live are characterized by relative constant rainfall, temperature, and humidity (Richards 1964), most lemurs are exposed to more marked seasonal fluctuations in climatic conditions (Morland 1993), which has been linked to the evolution of unique lemur traits (Wright 1999). Temperature was previously identified as a significant ecological constraint in primates (Bernstein 1972; Iwamoto and Dunbar 1983; Morland 1993; Nash 1998; Ostner 2002). When ambient temperatures fall below a critical threshold, homeotherms have to use proportionately more energy to maintain body temperature (Kleiber 1961; Schmidt-Nielson 1997). Several behavioral (e.g. reduced activity), postural (e.g. hunching) and social activities (e.g. huddling) serve as thermoregulatory mechanisms in lemurs (Morland 1993) and seasonal variation in temperature can be a significant metabolic stressor affecting glucocorticoids excretion in wild primates (Weingrill et al. 2004; Beehner and McCann 2008; Gesquiere et al. 2008). *Lepilemur leucopus* was seasonally affected by cold stress as evidenced by an increase in resting time (Chapter 2), but also by an increase in metabolizable energy intake at lower ambient temperatures (Chapter 4). The importance of temperature and thermoregulation has received little attention in primate nutritional ecology calling for more studies on this topic. For example, a deficiency in micronutrients may render an individual unable to maintain body temperature adequately under cold stress (Topping et al. 1980; Beard et al. 1990; Hall et al. 1990) and should have a direct influence on food selection.

Given the relatively high cost of female reproduction in mammals, do food selection and behavior differ between sexes in a sexually monomorphic primate?

A sex-specific asymmetry in reproductive resource allocation exists through internal offspring development, lactation and parental care of dependent offspring by females (Clutton-Brock 1991). Nevertheless, males and females of *L. leucopus* did not differ in their nutrient or energy intake regardless of female reproductive state (Chapter 4). Similarly, females of *Lemur catta* (ring-tailed lemurs) do not differ from males in feeding behavior or nutrient intake (Gould et al. 2011). Gestation length and lactation periods are longer in primates compared to non-primate mammals (Dufour and Sauther 2002; Derrickson 1992), resulting in a reduction of daily nutrient transfer from mother to infant (Gould 2011). *Lemur catta* produces relatively dilute milk of low protein, fat and energy content, minimizing daily energetic costs to females (Tilden and Oftedal 1997). While no information on the milk composition of sportive lemurs is available, but can expected to be high in nutrient and energy density given the fact that they park their infants and suckling occurs infrequently (Tilden and Oftedal 1997), lactation costs may be offset by reduced energy expenditure in physical activity in *L. leucopus* females during the lactation period (Chapter 4). Information on sex-specific energy and nutrient intake, especially in monomorphic primates, is still scarce. However, equally high energetic costs to males may be a general feature of mammalian reproduction (Lane et al. 2010).

Female dominance, in which females are agonistically dominant to males in all behavioral contexts, is rare among mammals and primates in general, but common in lemurs (Kappeler 1993), including sportive lemurs (Rasoloharijaona et al. 2008; Hilgartner et al. 2012). Female dominance may have evolved to ensure priority of access to food to cope with high reproductive costs in a seasonal environment (Wright 1999; Jolly 1984). Sex differences in foraging related to reproduction are expected consequences of female dominance theory (Hemmingway 1999). Lack of intersexual differences in macronutrient intake across all female reproductive stages (Chapter 4) contradicts the idea that female dominance in *L. leucopus* may be related to a female strategy of ensuring adequate access to limited food supply. Similarly, female dominance in *L. catta* is not related to physiological state (Rasamimanana et al. 2006). Detailed comparative data on metabolic strategy such as energy storage and mobilization, nutritional ecology and reproduction are needed to further our understanding of the adaptive significance of female dominance (Pereira et al. 1999).

As primates tend to choose proteinaceous foods (Conklin-Brittain et al. 1998; Oftedal 1991; Hanya and Bernard 2012) and as the average protein-to-fiber ratio of mature leaves correlates positively with primate biomass (Chapman et al. 2004; Ganzhorn 1992; Ganzhorn et al. 2009; Oates et al. 1990), primate reproductive success seems to be influenced by protein availability (Vogel et al. 2012). Nevertheless, protein intake was not increased in females during the lactation period in *L. leucopus* (Chapter 4). However, the relative contribution of macronutrients may be more important than total intakes

(Raubenheimer et al. 2009; Simpson et al. 2010). In addition, adequate nutrition requires also sufficient quality of protein, i.e. an appropriate amino acid composition to allow for normal biological function (Leonard 2000). The lactation period of *L. leucopus* was characterized by a dominance of young leaves (Chapter 2). Amino acid content and, hence, nutritive status of leaves differ with leaf maturation (Journet and Cochrane 1978; Roy et al. 2013). Investigations of amino acid profiles of wild primate foods are rare. However, Curtis (2004) investigated amino acid intake by *Eulemur mongoz* (mongoose lemurs) and found that immature leaves were richer in essential amino acids than mature leaves. Future studies should not only consider protein quantity but also protein quality of wild foods by estimating amino acid composition to further our understanding of dietary strategies.

How can small-bodied folivorous primates cope with a diet that can be considered deviant for the given body size?

Although most arboreal folivores are relatively large allowing them to handle large quantities of food of low caloric and nutritional density (McNab 1978), folivory is also observed in some small-bodied primate species of less than 1 kg body mass. Since the relative energy requirements increase with decreasing body size (Nagy 1987), small-bodied folivores can be expected to display special physiological and/or behavioral adaptations to deal with/overcome energetic constraints. Nevertheless, sportive lemurs combine folivory with a primarily saltatory, and hence energetically expensive, locomotion (Warren and Crompton 1997). In addition, sportive lemurs are active at night when low ambient temperatures may increase thermoregulatory demands during the cold dry season (Willmer et al. 2000; Chapter 4). By comparing daily energy intake of *L. leucopus* with field metabolic rates previously measured in a congener (red-tailed sportive lemur, *L. ruficaudatus*; Schmid and Ganzhorn 1996), sportive lemurs seem to be able to meet their energy requirements (Chapter 4). Sportive lemurs depress their metabolic rate even further than the already low rates expected for folivorous mammals in general (Ganzhorn 1992; Schmid and Ganzhorn 1996) and reduce costs of locomotion by remarkably short nightly travel distances (Warren and Crompton 1997). In addition, *L. leucopus* ingested large amounts of food to satisfy their nutritional requirements (Chapter 4), probably facilitated by selective retention of solutes and fine particles of digesta in the hindgut and more rapid excretion of coarse fibrous material (Foley and Cork 1992, Cork 1994, Nash 1998). Furthermore, as *L. leucopus* fed predominantly on the most common plant species (Chapter 2), it followed a strategy of energy acquisition at low foraging costs (Norscia 2012; Simmen 2014). However, to better understand what seasons are energetically limiting (Ganzhorn 2002; Ganzhorn 2004) further studies should estimate seasonal energy intake together with energy expenditure (Krockenberger 2003) or measure seasonal energy balance (Grueter et al. 2014).

Not only relative energy but also protein requirements increase with decreasing body size (Sakaguchi 2003). However, determining the precise protein requirements of wild primates is difficult because it requires experimental studies that include nutritional manipulation (Chapman et al. 2012). Requirements for captive primates are calculated from individuals fed a high-quality reference protein (Oftedal 1991). However, each particular natural food may be deficient in some amino acids and wild primates need higher protein levels than those of captive individuals to acquire a balanced set of amino acids (Simmen et al. 2007). In addition, the conventional factor of 6.25 to convert nitrogen into crude protein likely overestimates dietary protein concentration in tropical leaves (Milton and Dintzis 1981; Conklin-Brittain et al. 1999). *Lepilemur leucopus* prioritized protein over non-protein intake, indicating that dietary protein may be in limited supply (Chapter 4). In addition, *L. leucopus* practices cecotrophy (Hladik 1978), a nutritional strategy that enhances protein and amino acid utilization (Hintz 1969; Sakaguchi 2003). However, more detailed studies on the cecotrophy behavior of *L. leucopus* are required to understand its relative importance to nutrient gain. Furthermore, new non-invasive methods are available to investigate nitrogen imbalance in wild primates (Vogel et al. 2012), promising new insights into dietary adaptations of small-bodied folivores.

Conclusions

Lepilemur leucopus seems to be able to overcome energetic constraints imposed by a low-quality diet despite small body size through various adaptive mechanisms. Although some folivorous primates experience behavioral and physiological effects of food limitation (Harris et al. 2009), there was no consistent evidence that seasonal decrease in food quantity had a major impact on feeding behavior, activity patterns or social interactions in *L. leucopus*. Instead, feeding stress seems to be more related to food quality, such as availability of dietary protein, than food quantity. As *L. leucopus* forages solitarily even though its diet does not place constraints on group foraging, top-down processes seem to be more important than bottom-up processes in shaping its social system. However, further studies are needed to quantify the impact of varying levels of predation pressure on the nature of social relationships in *L. leucopus*.

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APPENDICES

Appendix A Summary of continuous focal animal observations conducted simultaneously on adult male and female range-mates of *L. leucopus* throughout the year (Season: 1 = early wet, 2 = late wet, 3 = early dry, 4 = late dry). The calendar date is given as day-month-year.

Social unit	Date	Season	**female**	hours	**male**	hours
1	05.11.2011	1	**f1B**	10:13:26		
1	08.01.2012	1	**f1B**	9:22:17		
1	21.02.2012	2	**f1B**	9:41:13		
1	05.06.2012	3	**f1B**	11:31:46	**m10**	11:00:02
1	11.07.2012	3	**f1B**	10:36:17	**m10**	10:58:23
1	26.08.2012	4	**f1B**	9:52:43	**m10**	10:48:33
1	04.10.2012	4	**f1B**	9:57:08	**m10**	8:52:39
2	23.10.2011	1	**f2**	10:23:35		
2	05.12.2011	1	**f2**	9:35:30	**m9**	10:05:03
2	06.02.2012	2	**f2**	8:43:11	**m9**	9:59:52
2	23.03.2012	2	**f2**	10:51:56	**m9**	10:01:42
2	09.05.2012	3	**f2**	10:15:40	**m9**	11:09:34
2	27.06.2012	3	**f2**	11:12:43	**m9**	11:30:45
2	17.08.2012	4	**f2**	10:52:33	**m9**	11:08:09
2	26.09.2012	4	**f2**	10:39:33	**m9**	10:32:36
3	23.12.2011	1	**f3**	8:55:11	**m3**	9:27:30
3	31.03.2012	2	**f3**	9:40:59	**m3**	9:35:58
3	04.05.2012	3	**f3**	10:54:01	**m3**	10:12:30
3	23.06.2012	3	**f3**	9:58:28	**m3**	11:24:59
3	01.08.2012	4	**f3**	11:04:32	**m3**	10:57:07
3	12.09.2012	4	**f3**	10:08:31	**m3**	11:03:17
4	13.12.2011	1	**f4**	8:59:38	**m4**	9:19:01
4	25.01.2012	1	**f4**	9:57:12	**m4**	10:23:16
4	19.03.2012	2	**f4**	11:07:14	**m4**	11:53:16
4	30.04.2012	2	**f4**	11:43:01	**m4**	11:57:32
4	18.06.2012	3	**f4**	12:07:22	**m4**	12:35:29
4	25.07.2012	3	**f4**	11:00:38	**m4**	11:47:10
4	08.09.2012	4	**f4**	11:03:23	**m4**	11:19:02
4	18.10.2012	4	**f4**	10:24:15	**m4**	10:35:59
5	23.11.2011	1	**f5**	9:57:44	**m5**	9:56:24
5	03.01.2012	1	**f5**	9:35:30	**m5**	9:38:24
5	25.02.2012	2	**f5**	10:29:40	**m5**	10:37:44
5	09.04.2012	2	**f5**	11:26:57	**m5**	11:12:07
5	10.06.2012	3	**f5**	12:15:05	**m5**	12:35:24
5	15.07.2012	3	**f5**	12:08:52	**m5**	12:00:20
5	30.08.2012	4	**f5**	11:27:43	**m5**	10:52:24
6	09.12.2011	1	**f6**	9:44:33	**m6**	9:38:39
6	10.02.2012	2	**f6**	10:22:28	**m6**	9:34:37
6	27.03.2012	2	**f6**	11:21:19	**m6**	11:22:33
6	30.05.2012	3	**f6**	12:26:08	**m6**	12:17:21
6	02.07.2012	3	**f6**	12:21:02	**m6**	12:07:54
6	21.08.2012	4	**f6**	11:32:52	**m6**	11:19:12
6	30.09.2012	4	**f6**	12:00:46	**m6**	10:53:25
7	18.11.2011	1	**f7**	9:29:35	**m7**	9:57:00
7	21.01.2012	1	**f7**	9:36:58	**m7**	9:50:44
7	04.03.2012	2	**f7**	10:20:57	**m7**	10:40:44
7	25.04.2012	2	**f7**	11:46:32	**m7**	11:47:35
7	14.06.2012	3	**f7**	12:27:43	**m7**	12:41:50
7	20.07.2012	3	**f7**	11:53:03	**m7**	12:24:17
7	03.09.2012	4	**f7**	10:43:39	**m7**	11:21:36
7	12.10.2012	4	**f7**	10:42:20	**m7**	10:39:13

Appendix B Summary of continuous focal animal observations (hours = time in sight) conducted throughout the year on the focal animals belonging to seven social units of Lepilemur leucopus (Season: 1 = early wet, 2 = late wet, 3 = early dry, 4 = late dry).

Social unit	Date	Season	**female**	hours	**male**	hours
1	05.11.2011	1	**f1B**	10:13:26		
1	08.01.2012	1	**f1B**	9:22:17		
1	21.02.2012	2	**f1B**	9:41:13		
1	21.04.2012	2	**f1B**	11:08:29		
1	05.06.2012	3	**f1B**	11:31:46	**m10**	11:00:02
1	11.07.2012	3	**f1B**	10:36:17	**m10**	10:58:23
1	26.08.2012	4	**f1B**	9:52:43	**m10**	10:48:33
1	04.10.2012	4	**f1B**	9:57:08	**m10**	8:52:39
2	23.10.2011	1	**f2**	10:23:35		
2	05.12.2011	1	**f2**	9:35:30	**m9**	10:05:03
2	06.02.2012	2	**f2**	8:43:11	**m9**	9:59:52
2	23.03.2012	2	**f2**	10:51:56	**m9**	10:01:42
2	09.05.2012	3	**f2**	10:15:40	**m9**	11:09:34
2	27.06.2012	3	**f2**	11:12:43	**m9**	11:30:45
2	17.08.2012	4	**f2**	10:52:33	**m9**	11:08:09
2	26.09.2012	4	**f2**	10:39:33	**m9**	10:32:36
3	14.11.2011	1			**m3**	8:34:09
3	23.12.2011	1	**f3**	8:55:11	**m3**	9:27:30
3	01.11.2011	1	**f3**	10:22:56		
3	02.02.2012	1			**m3**	7:34:06
3	13.03.2012	2	**f3**	9:55:23		
3	31.03.2012	2	**f3**	9:40:59	**m3**	9:35:58
3	04.05.2012	3	**f3**	10:54:01	**m3**	10:12:30
3	23.06.2012	3	**f3**	9:58:28	**m3**	11:24:59
3	01.08.2012	4	**f3**	11:04:32	**m3**	10:57:07
3	12.09.2012	4	**f3**	10:08:31	**m3**	11:03:17
4	13.12.2011	1	**f4**	8:53:26	**m4**	8:23:19
4	25.01.2012	1	**f4**	9:20:19	**m4**	9:19:43
4	19.03.2012	2	**f4**	10:39:27	**m4**	10:02:49
4	30.04.2012	2	**f4**	10:19:40	**m4**	11:24:32
4	18.06.2012	3	**f4**	11:38:01	**m4**	12:00:43
4	25.07.2012	3	**f4**	9:55:08	**m4**	11:27:02
4	08.09.2012	4	**f4**	10:41:58	**m4**	10:43:59
4	18.10.2012	4	**f4**	10:11:10	**m4**	10:26:48
5	23.11.2011	1	**f5**	9:19:56	**m5**	9:22:27
5	03.01.2012	1	**f5**	8:43:59	**m5**	8:34:58
5	25.02.2012	2	**f5**	9:25:49	**m5**	7:11:39
5	09.04.2012	2	**f5**	10:16:38	**m5**	10:41:26
5	10.06.2012	3	**f5**	11:26:29	**m5**	11:43:06
5	15.07.2012	3	**f5**	11:28:27	**m5**	11:19:01
5	30.08.2012	4	**f5**	10:49:42	**m5**	10:38:59
5	08.10.2012	4	**f5**	10:38:38	**m5**	10:22:12
6	27.10.2011	1	**f6**	10:30:56		
6	09.12.2011	1	**f6**	9:34:32	**m6**	9:21:22
6	28.12.2011	1			**m6**	8:24:32
6	10.02.2012	2	**f6**	8:54:54	**m6**	7:57:50
6	27.03.2012	2	**f6**	10:36:20	**m6**	10:41:52
6	30.05.2012	3	**f6**	11:29:25	**m6**	9:56:14
6	02.07.2012	3	**f6**	11:13:23	**m6**	11:19:13
6	21.08.2012	4	**f6**	11:08:09	**m6**	10:46:40
6	30.09.2012	4	**f6**	11:46:49	**m6**	9:59:26
7	18.11.2011	1	**f7**	9:12:27	**m7**	9:28:42
7	21.01.2012	1	**f7**	9:12:05	**m7**	7:59:54
7	04.03.2012	2	**f7**	9:54:23	**m7**	10:23:34
7	25.04.2012	2	**f7**	11:06:15	**m7**	11:05:35
7	14.06.2012	3	**f7**	12:01:14	**m7**	11:57:52
7	20.07.2012	3	**f7**	10:49:22	**m7**	12:12:28
7	03.09.2012	4	**f7**	10:34:57	**m7**	11:01:25
7	12.10.2012	4	**f7**	10:28:29	**m7**	10:20:33

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DECLARATION

I hereby declare that I have written this thesis entitled “Behavioral and Feeding Ecology of a Small-bodied Folivorous Primate (*Lepilemur leucopus*)” independently and with no other aids or sources than quoted.

Iris Dröscher

Göttingen, 05.11.2014