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Environmental and Individual Determinants of Parasite Richness Across Seasons in a Free-Ranging Population of Mandrills (*Mandrillus sphinx)*

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Objectives: Parasites are ubiquitous and evolve fast. Therefore, they represent major selective forces acting on their hosts by influencing many aspects of their biology. Humans are no exception, as they share many parasites with animals and some of the most important outbreaks come from primates. While it appears important to understand the factors involved in parasite dynamics, we still lack a clear understanding of the determinants underlying parasitism. In this 2-year study, we identified several factors that influence parasite patterns in a wild population of free-ranging mandrills (*Mandrillus sphinx)*.

Methods: We explored the potential impact of seasonal factors—rainfall and temperature—and host characteristics, including sex, age, rank, and reproductive status, on parasite richness. We analyzed 12 parasite taxa found in 870 fecal samples collected from 63 individuals. Because nematodes and protozoa have different life-cycles, we analyzed these two types of parasites separately.

Results: Contrary to other studies where humid conditions seem favorable to parasite development, we report here that rainfall and high temperatures were associated with lower nematode richness and were not associated with lower protozoa richness. In contrast, female reproductive status seemed to reflect the seasonal patterns found for protozoa richness, as early gestating females harbored more protozoa than other females. Sex and dominance rank had no impact on overall parasite richness. However, age was associated with a specific decrease in nematode richness.

Conclusion: Our study emphasizes the need to consider the ecological context, such as climatic conditions and habitat type, as well as the biology of both parasite and host when analyzing determinants of parasite richness. Am J Phys Anthropol 159:442–456, 2016.

Wild animals are naturally exposed to a large array of parasites throughout their lives. The number of different parasite species is staggering. For example, there are between 75,000 and 300,000 different helminth species that are parasites of vertebrates (Dobson et al., 2008). Even if death only rarely results from primary effects of parasitism, parasites often induce detrimental consequences to their hosts (O'Donnell, 1997), e.g., by altering general metabolism, immune functions, food intake or by increasing predation risk (Dobson and Hudson, 1992, 1995; Hudson et al., 1992; Coop and Holmes, 1996; Milton, 1996; Morand and Harvey, 2000; Lello et al., 2005). As a result, parasites generate a persistent selection pressure that also impacts life history traits of the host, such as longevity or reproduction (Minchella, 1985; Kirchner and Roy, 1999; Simková et al., 2008). Parasitism could also affect large-scale evolutionary processes. For instance, parasite richness is positively associated with phylogenetic diversity among primates (Nunn et al., 2004) and parasites play a role in the evolution of sociality (Kappeler and Van Schaik, 2001; Kappeler et al., 2015). Finally, through the detrimental effects imposed on their hosts, parasites can have a significant impact on population dynamics, putting small populations of endangered species particularly at risk (Nunn et al., 2015). Parasites are therefore considered a major threat in conservation biology (Mccallum and Dobson, 1995; Thompson et al., 2010). In fact, malaria is responsible for the decline and extinction of many native Hawaiian bird species (Elliott et al., 2010), while distemper virus has almost led to the extinction of black-footed ferrets (Thorne and Williams, 2012) and caused the death of one third of the population of Serengeti lions (Cleaveland et al., 2000). Understanding which factors influence parasitism in wild populations is therefore crucial for both scientific and conservational purposes.

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Determinants of parasitism are particularly interesting to study in the primate order. First, primates live in variable environments, ranging from deserts to equatorial rainforests and therefore harbor a large array of different parasite species. For example, 136 different helminth species have been found in 69 species of primates (Vitone et al., 2004). Second, according to the IUCN red list, nearly half of all primates are threatened. Decreased home range sizes following forest fragmentation increases density and home range overlaps, enhancing both socially- and environmentally-mediated infection risks (Gillespie and Chapman, 2008). Third, primates are our closest biological relatives. This close phylogenetic relationship with humans results in a high potential for cross-species transmission of parasites (Calvignac-Specer et al., 2012). Some of the most virulent emerging infectious diseases found in humans, such as AIDS or Ebola, have shifted from wild primate populations to humans (Pedersen and Davies, 2010). With increasing habitat fragmentation and bushmeat trade, contacts between natural primate populations and human settlements have become more frequent (Chapman et al., 2005) and studies of parasitism in wild primate populations may contribute to an assessment of the risks of parasite spillover in both directions.

Because fecal samples offer an easy and noninvasive way to assess individual parasite status throughout time, communities of gastrointestinal parasites in primates have already been studied in detail (eastern chimpanzees *Pan troglodytes schweinfurthii*: McGrew et al., 1989; Muehlenbein, 2006; Gillespie et al., 2010; chacma baboons *Papio ursinus*: Benavides et al., 2012; yellow baboons *Papio cynocephalus*: Hausfater and Meade, 1982; olive baboons *Papio anubis*: Müller-Graf et al., 1996; mantled howler monkeys *Alouatta palliata*: Valdespino et al., 2010; brown howler monkeys *Alouatta fusca*: Stuart et al., 1993; eastern red colobus *Procolobus rufomitratus*: Chapman et al., 2007; rhesus macaques *Macaca mulatta*: Knezevich, 1998; yakushima Japanese macaques *Macaca fuscata yakui*: MacIntosh et al., 2010; white-faced capuchins *Cebus capucinus*: Parr et al., 2013; red-fronted lemurs *Eulemur fulvus rufus*: Clough et al., 2010). A wide range of factors have been found to impact parasitism, including environmental variables, species characteristics, population factors, and individual host traits (Tompkins et al., 2011). For example, seasonal variation in rainfall and temperature both strongly influence parasite population dynamics. Humid and hot environments usually favor parasite development and transmission rates (Nunn and Alitzer, 2006). However, seasonal variation in parasite richness or abundance can also arise from processes including host behavior, reproduction, or immune function (Altizer et al., 2006). Host density, group size, home range size or diet (Nunn et al., 2003; Nunn and Dokey, 2006) have all been proposed to influence parasitism along with several individual host traits including sex, age, body mass, reproductive status, dominance rank, network centrality, and hormone levels (Nunn and Alitzer, 2006).

Additional comparative data from understudied species such as rainforest primates can contribute to a better understanding of complex parasite population dynamics in wild host populations because tropical habitats and low latitudes are favorable to parasites (Guernier et al., 2004). In this study, we examined the influence of several environmental and individual traits on gastrointestinal parasite richness in a natural population of mandrills (*Mandrillus sphinx*). We chose to analyze determinants of parasite richness rather than determinants of specific parasite prevalence because hosts are naturally co-infected with several parasite species that have possible synergistic effects. Consequently, focusing on each parasite separately is not informative regarding the complexity of parasite infections in wild populations (Bordes and Morand, 2009). In contrast, parasite richness is often considered a more robust metric than parasite prevalence or abundance. It is also a pertinent indicator of the ability of hosts to struggle against multiple parasite infections (Muehlenbein and Watts, 2010). Mandrills are semiarboreal, omnivorous, Old World primates that live in dense equatorial forests of Central Africa, where parasite diversity is high. Although they live in wooded environments interspersed with savannas, they generally strongly avoid open habitats. They form large groups numbering several hundreds of individuals (Abernethy et al., 2002). Transmission risk and parasite prevalence are therefore expected to be high in wild mandrill populations. In line with this, several nematode and protozoa taxa have been reported in captive mandrills (Setchell et al., 2007). Here, we studied patterns of parasite richness in 63 individuals during a 24-month study. Despite being direct life-cycle parasites (i.e, with no intermediate host), nematodes and protozoa exhibit notable differences regarding their developmental stages. On the one hand, nematodes, despite showing different transmission modes (i.e., oral ingestion; skin penetration), share a common feature across species: they are all long life-cycle parasites. When emitted in the feces, eggs are not immediately infectious but rather need to undergo further developmental stages, generally for around two weeks (Neveu-Lemaire, 1952) in the environment before being infectious to other hosts. Protozoa, on the other hand, are short life-cycle parasites, they are immediately infective when emitted in fecal material and may thus be transmitted by direct physical contacts between individuals through the classical oro-fecal route. With such contrasting life histories, we expected that risk of infection by these two types of parasites would depend on different determinants. In this study, we thus analyzed nematodes and protozoa separately. In particular, we attempted to identify the different factors underlying seasonal fluctuations. These patterns possibly reflect the influence of several biologically distinct mechanisms on host-parasite interactions (Altizer et al., 2006). Among other kind of factors, environmental factors such as climatic conditions are season-dependent. In addition, individual status also changes seasonally. For example, the reproductive status of females varies across seasons and may impact parasite susceptibility, explaining (at least partially) seasonal variation of parasite richness. Therefore, we analyzed the influence of the variation in rainfall and temperature on parasite richness, as well as the impact of host sex, age, dominance rank, and female reproductive status. Table 1 summarizes the predictions we made based on existing literature. As expected, we found contrasting seasonal and individual effects between these two sets of parasites infecting free-ranging mandrills.

MATERIAL AND METHODS

Ethical statement

This study complies with ethical protocols approved by the CENAREST institution (authorization number:

TABLE 1. A summary of the existing literature on the relationship between parasitism and various determinants in primates and related hypotheses

Determinant	Correlation	Predictions	Evidences from primate field studies	Hypotheses in mandrills
Rainfall and temperature	Both positive	Encounter rate: Moist environment and high temperatures generally favor parasite development and survival (Nunn and Alitzer, 2006).	Chacma baboons (richness; Benavides et al., 2012); eastern chimpanzees (nematode prevalence; Gillespie et al., 2010).	H1: Positive impact of rainfall and temperature on nematode richness alone because of free-living stages in the environment.
Sex	Male-biased parasitism	Inequities in immunity: Higher susceptibility in males resulting from immunosuppressive effects of steroid hormones (Zuk and Mckean, 1996; Klein, 2000, 2004; Verthelyi, 2001). Encounter rate: Higher food intake in males increases exposure to parasites transmitted by ingestion of free-living stages from the environment (Nunn and Alitzer, 2006; Cross et al., 2009). In sexually dimorphic species, larger body size in males may provide larger habitat for parasite colonization (Vitone et al., 2004; Cross et al., 2009).	Rhesus macaques (richness and intensity; Knezevich, 1998).	H2: Male-biased parasitism because of a strong sexual dimorphism and testosterone excretion in males (Setchell and Wickings, 2005).
	Female-biased parasitism	Inequities in immunity: Higher susceptibility in females resulting from immunosuppressive effects of hormones produced during gestation (Szekeres-bartho, 1997; Klein, 2004).	Chacma baboons (richness; Benavides et al., 2012); red-fronted lemurs (protozoa intensity; Clough et al., 2010).	H3: Gestating females are more parasitized by both set of parasites.
Dominance rank	High-ranking biased parasitism	Encounter rate: Higher food intake in dominant individuals than in subordinates increases exposure to parasites transmitted by ingestion of free-living stages from the environment (Nunn and Alitzer, 2006). Inequities in immunity: Higher susceptibility in dominant individuals resulting from immunosuppressive effects of steroid hormones (Sapolsky, 2005).	Eastern chimpanzees (nematode richness and intensity; Muehlenbein and Watts, 2010); Japanese macaques (nematode richness; MacIntosh et al., 2012); yellow baboons (nematode intensity in males; Hausfater and Watson, 1976).	H4: High-ranking males harbor higher parasite richness because males hierarchy is unstable and dominant males exhibit higher testosterone levels than low-ranking males (Setchell et al., 2008).
	Low-ranking biased parasitism	Inequities in immunity: In stable rank societies, higher susceptibility in subordinates resulting from immunosuppressive effect of glucocorticoid hormones (Sapolsky, 2005).		
Age	Positive	Encounter rate: Accumulation of parasites throughout host lifetime because parasite encounter increases with host age (Nunn and Alitzer, 2006).	Eastern chimpanzees (richness; Gillespie et al., 2010); white-faced capuchins (richness; Parr et al., 2013)	H5a: Positive correlation.

TABLE 1. Continued

Determinant	Correlation	Predictions	Evidences from primate field studies	Hypotheses in mandrills
	Negative	Inequities in immunity: Reinforced immunity in adults.	Japanese macaques (nematode richness in females; MacIntosh et al., 2012); yellow baboons (prevalence and intensity of *Strongyloides sp.*; Müller-Graf et al., 1996).	H5b: Negative correlation.
	Not linear	Adaptive immunity: Parasitism initially increases and then decreases with resistance acquisition (Hudson and Dobson, 1995; Cornell et al., 2008).	Chacma baboons (richness; Benavides et al., 2012).	H5c: Convex relationship.

AR0001/14/MESRSC/CENAREST/CG/CST/CSAR). This research adhered to the legal requirements of Gabon and to the American Society of Primatologists principles for the ethical treatment of nonhuman primates.

Study population

This 24-month study (July 2012–June 2014) was conducted on a free-ranging mandrill population living in a 116 km^2 fenced private park (Lékédi Park), with little human disturbance, near the village of Bakoumba, in Southern Gabon (570 m above sea level; 13°01′E, 1°49′S). The population was founded in 2002 when 36 individuals originating from a semi-captive population housed at the CIRMF (Centre International de Recherches Médicales de Franceville) were released into the Lékédi Park (for details, see Peignot et al., 2008). In 2006, 29 additional individuals were released into the initial group. Adult females were seen cycling shortly after the release. Wild immigrant males joined the group starting in 2003 and reproduced with captive-born females (Peignot et al., 2008). In July 2012, over 80% of the population was composed of wild-born animals.

From 2002 to 2012, mandrills were supplemented with bananas and monkey chows in limited quantities to improve their diet. At the very beginning, food was provided three to four times a week but the pace decreased rapidly to occasional supplementations (on average once or twice a week). This supplementation was stopped in April 2012 (3 months before the beginning of our study). This initial supplementation was never meant to fulfill the caloric needs of the mandrills and presumably did not influence their physical condition nor impacted the parasitism patterns of the population. Since 2004, tourists have regularly visited the group (on average one visit per week), allowing released mandrills to remain habituated to human presence. Tourist visits decreased progressively since 2012 and ceased completely in June 2014, when another group of mandrills, which serves touristic purposes only, was released far from the home range of the studied population.

A long-term field project was established in January 2012 to study this free-ranging mandrill population ("Mandrillus Project": www.projetmandrillus.com). Field assistants were trained and habituation and monitoring programs started. At the very beginning of the Mandrillus Project, observers only spent a few hours per day with the group, but this duration increased progressively thanks to daily contacts with the animals. The group is now followed every day from 6:00 am to 6:00 pm. In addition, fecal samples from identified animals are collected opportunistically. In 2014, the population comprised about 120 to 140 habituated individuals (for details on the population, see Brockmeyer et al., 2015). The mandrills occupy a home area of 866 ha that exceeds the park's boundaries, as they may spend weeks outside the park. Indeed, the park's fences have never constituted a restraint on animal movements (see Fig. 3 in Brockmeyer et al., 2015). Moreover, other wild mandrill groups of unknown sizes are known to live in the park but we have never witnessed intergroup encounters.

Fecal collection and parasite identification

During the study period, we collected 870 fecal samples from 63 nonambiguously identified individuals of both sexes (33 females, 30 males) and all ages (mean:

7.56, range: 1–20 years), just after defecation. In the field, we systematically collected whole fecal samples that were then stored at 4°C until analyses. Coprological analyses were performed as follows in the field laboratory located in the village of Bakoumba, near the park. We first mixed collected samples to homogenize the presence of gastrointestinal parasites and concentrated the parasites using sedimentation methods. Two to 3 g of stool were placed in a mixing chamber with 6 ml of Bailanger solution (15 g sodium acetate, 3.60 ml acetic acid, 1,000 ml distilled water) and mixed for 15 s with a vortex until complete homogenization. A filter and a sedimentation chamber were attached to the mixing chamber and the solution was centrifuged at 1,500 rpm for 3 min. The supernatant was then removed and, after homogenization of the sediment, we examined a drop of the suspension under a microscope at 100×, followed by 400×, and 1,000× for parasite identification.

Using a micrometer, but without staining, we classified nematode eggs and protozoa trophozoites and cystic stages by taxon according to morphological characteristics based on shape, content and size of the eggs and cystic stages (Deluol et al., 1998, 1999; see Table 2 for the criteria used to identify protozoa). However, some of the found taxa corresponded to undistinguishable species. First, eggs from some nematodes belonging to the Rhabditida order are similar and exact identification would have required culture of the eggs from each fecal sample, which is hardly practical in the field. We therefore considered complexes of *Strongyloides* sp. and *Trichostrongylus* sp. morphotypes. Second, the distinction between *Entamoeba histolytica* and *Entamoeba dispar* is only possible using laboratory tests. We therefore grouped them into a "*E. histolytica*/*dispar* complex." The impossibility to determine exactly how many species are included in these taxa constitutes a limitation of our study because parasite richness may be underestimated. However, we do not think that this limitation has influenced our results in any given, nonrandom, direction.

We did not precisely weigh the portion of analyzed feces because we performed qualitative analyses. Indeed, quantification of protozoa is challenging: each sample contains hundreds/thousands of cysts per species, allowing confident species identification for a given sample, while particular individual cysts are sometimes not identifiable, especially among small amoeba species. Quantitative analyses of protozoa would have therefore required an accurate identification of each individual parasite form, leading to increased error risks. Quantification of nematodes is less difficult, but the number of parasite forms released in fecal material is not always an accurate estimate of the intensity of the infection, particularly with a limited number of fecal samples per individual (Muehlenbein and Watts, 2010). However, even when performing qualitative analyses only, we cannot exclude that false negatives may have occurred, particularly for samples containing only a few nematode eggs.

Fifty percent of the fecal samples were analyzed within 24 h of collection and 74% were analyzed from 0 to 7 days after collection. Some samples (15.7%) were analyzed 2 to 4 weeks following collection. For protozoa, cystic stages are stable and persistent within the fecal samples. Therefore, a 1-month delay between sampling and subsequent analysis does not affect parasite identification. In contrast, nematode eggs still grow and undergo larval development in the fecal samples after emission (Neveu-Lemaire, 1952). Because nematode species are difficult to identify from larvae, a longer delay than the maturation time of nematode eggs could hamper parasite identification. Thus, for nematodes, we only considered fecal samples analyzed within a window of 2 weeks following emission, which is the average time for eggs to develop into larvae (Neveu-Lemaire, 1952). We thus analyzed a restricted dataset for nematodes ($N = 759$ fecal samples). To further confirm that the delay between collection and analysis did not influence our results, we re-ran our statistical analyses using the fecal samples analyzed within 3 days of collection only. We obtained the same results, but with weaker relationships due to more limited sample sizes (results not shown).

Statistical analyses

Because they demonstrate contrasting life histories, we analyzed nematode and protozoa richness separately. For these two sets of species, we ran two types of analyses: individual-centered analyses and population-centered analyses. At the individual level, we defined the monthly parasite richness per animal by calculating the average number of parasite species found in the samples collected on a same individual over a 1-month period. We chose to restrict our analyses to the months where at least three fecal samples were available per animal. Indeed, considering less than three samples limits the ability to detect accurate infectious status because of a non-negligible probability of false negatives (due to e.g., intermittent excretion of parasites). For instance, it has been shown that three to four samples per individual, collected on nonconsecutive days, are necessary to accurately diagnose intestinal infection in wild chimpanzees (Muehlenbein, 2005). Following this restriction, we analyzed a subset of 471 fecal samples for nematodes, and 553 fecal samples for protozoa. At the population level, we evaluated the weekly average parasite richness of all sampled individuals. We only considered the weeks where at least five different individuals were sampled. In this second set of analyses, we thus analyzed 732 fecal samples for nematodes and 812 fecal samples for protozoa. The same animals were sampled more than once within some weeks. For these individuals, we first considered weekly individual parasite richness, because important biases in estimating parasite richness may occur when the number of samples is considered instead of the number of individuals (e.g., pseudo-replication).

Individual-centered models. To examine the determinants of parasite richness, we first performed General Linear Mixed Models (LMM, nlme package, R) with a Gaussian error structure, as residuals were normally distributed. We conducted three different sets of models on the studied individuals.

1. The first set of models considered all sampled individuals (33 individuals: 19 females, 14 males; nematodes: mean ± SD: 5.0 ± 4.2 sampled individuals/month during 21 months and 4.5 ± 1.9 samples/individual/month; protozoa: mean ± SD: 5.3 ± 4.3 sampled individuals/month during 23 months and 4.5 ± 1.8 samples/individual/month). For these first models (nem1a and prot1a; Table 3), we investigated the effects of season (class variable, four modalities) and age

TABLE 2. Morphological criteria used to distinguish between cystic stages of protozoa without staining

Species	Size (μm)	Shape	Outline	Cytoplasma	Crystalloids	Nuclei
Balantidium coli	40–60	Round	Thick wall with (usually) visible cilia	Young cysts: vacuoles; old cysts: granular aspect	None	One kidney-shaped macronucleus; one adjacent micronucleus (usually not visible)
Entamoeba coli	15–20	Rounded or oval	Distinct, thick	Clear, hyalin, very refractive; two nuclei: one vacuole; four to eight nuclei: no vacuole	Needle-shaped (difficult to see)	One to eight nuclei; aggregated peripheral chromatin; thick, exentric karyosomes; cysts with two nuclei: the two nuclei are generally located each side of a vacuole; cysts with four to eight nuclei: nuclei are visible with adjustment
Entamoeba histolytica/dispar complex	12–14	Usually rounded, sometimes oval	Distinct but less thick than *E. coli* cysts	Granular; two nuclei: one vacuole; four nuclei: no vacuole	Sausage-shaped (irregular presence)	One to four nuclei; regular peripheral chromatin; central, punctiform karyosomes; cyst with two nuclei: the two nuclei are generally on the same side of a vacuole
Endolimax nana	8–10	Oval or rectangular	Distinct, slightly refractive	Hyalin	None	One to four nuclei; large visible karyosomes
Pseudolimax butschlii	8–15	All shapes	Thick, refractive	One vacuole	None	One nucleus; very large karyosome surrounded by a clear halo
Entamoeba hartmanni	6–10	Usually rounded	Distinct, refractive	Generally many small vacuoles	Sausage-shaped (irregular presence)	One to four nuclei; thick chromatin

The morphological criteria proposed come from Deluol et al. (1998, 1999).

TABLE 3. Description of the individual-centered models

Considered individuals	Sample size	Response variable	Individual-centered model	Explanatory variables
All individuals	$N = 104$ (471)	Monthly individual nematode richness	nem1a	~ Season + sex + age
			nem1b-rain	~ Rainfall + sex + age
			nem1b-temp	~ Temperature + sex + age
	$N = 122$ (553)	Monthly individual protozoa richness	prot1a	~ Season + sex + age
			prot1b-rain	~ Rainfall + sex + age
			prot1b-temp	~ Temperature + sex + age
Mature males	$N = 36$ (148)	Monthly individual nematode richness	nem2a	~ Season + age + rank
	$N = 42$ (175)	Monthly individual protozoa richness	prot2a	~ Season + age + rank
			prot2b-rain	~ Rainfall + age + rank
			prot2b-temp	~ Temperature + age + rank
Mature females	$N = 61$ (292)	Monthly individual nematode richness	nem3a	~ Season + age + rank
			nem3b-rain-T/G/L[a]	~ Rainfall + T/G/L[a] + age + rank
			nem3b-temp-T/G/L[a]	~ Temperature + T/G/L[a] + age + rank
	$N = 73$ (346)	Monthly individual protozoa richness	prot3a	~ Season + age + rank
			prot3b-rain-T/G/L[a]	~ Rainfall + T/G/L[a] + age + rank
			prot3b-temp-T/G/L[a]	~ Temperature + T/G/L[a] + age + rank
			prot3b-G1/G2-3[a]	~ G1/G2-3[a] + age + rank

[a] In different models, "T," "G," and "L" refer to the percentage of time spent in tumescence, gestation, and lactation for each considered month (respectively). "G1" and "G2-3" refer to the percentage of time spent in the first third and in the last two third of gestation for each considered month (respectively). Sample sizes given (N) indicate the number of lines of data. One line of data corresponds to parasite richness/individual/month. Numbers in parentheses represent the total number of fecal samples considered.

(continuous variable) and sex (class variable, two modalities; see below for a description of the explanatory variables) of the individual.

2. The second set of models considered males that were over 5 years old (12 males; nematodes: mean ± SD: 2.3 ± 1.4 sampled individuals/month during 16 months and 4.1 ± 1.3 samples/individual/month; protozoa: mean ± SD: 2.5 ± 1.5 sampled individuals/month during 17 months and 4.2 ± 1.4 samples/individual/month). For these second models (nem2a and prot2a; Table 3), we tested the effects of season and age and dominance rank (class variable, three modalities; see below) of the individual.
3. The third set of models was restricted to adult mature females over 4 years old (18 females; nematodes: mean ± SD: 3.1 ± 2.3 sampled individuals/month during 20 months and 4.8 ± 2.2 samples/individual/month; protozoa: mean ± SD: 3.3 ± 2.4 sampled individuals/month during 22 months and 4.7 ± 2.1 samples/individual/month). For these last models (nem3a and prot3a; Table 3), we also tested the effect of season and age and dominance rank of the individual (see below).

In all of these models, individual identity and year of sampling were considered as two random effects. Moreover, in preliminary analyses, we tested for a potential sampling bias by considering the number of coprological examinations performed per individual per month as an additional fixed factor. As this factor was consistently nonsignificant, we did not keep it in the selected models. We also performed preliminary models to test for a quadratic effect of age. As there was no evidence for such an effect, we did not consider this additional quadratic factor. For all three sets of analyses, we selected the final models that best fit our data using the Akaike Information Criterion (AIC) score. We found strong seasonal patterns in all final models (see Results). To explore the determinism of seasonality effects, we replaced the "season" variable by either the monthly cumulated rainfall or the monthly average temperature (continuous variables; see below), because both variables were correlated (all individuals: nem1b-rain, nem1b-temp, prot1b-rain, prot1b-temp; males: prot2b-rain, prot2b-temp; Table 3). In the set of models on mature females, we further tested for a potential effect of female reproductive cycle by considering the percentage of time spent in tumescence (T), lactation (L), or in gestation (G) per month. As these three variables were also highly correlated, we included them with either rainfall or temperature, in six additional models (nem3b-rain-T/G/L, nem3b-temp-T/G/L, prot3b-rain-T/G/L, prot3b-temp-T/G/L; Table 3). Finally, and because we found an effect of the time spent in gestation on protozoa richness, we performed two final models where the variable "time spent in gestation" was replaced by the percentage of time spent in the first trimester of gestation (G1), and in the second/third trimesters of gestation (G2-3), grouped together because of restricted sample sizes (prot3b-G1/G2-3; Table 3).

Population-centered models. To explore the influence of climatic conditions on parasite richness at the population level, we performed LMM with a Gaussian error structure, as residuals were normally distributed. We investigated the influence of different climatic variables on average weekly parasite richness in nematodes (59 individuals; mean ± SD: 8.8 ± 4.0 sampled individuals/week and 1.3 ± 0.6 samples/individual/week) and in protozoa (63 individuals; mean ± SD: 9.1 ± 4.3 sampled individuals/week and 1.3 ± 0.6 samples/individual/week). Alternatively, we explored the effects of cumulated and maximal rainfalls and the effects of average and maximal temperatures recorded during the week of collection (continuous variables; see below) in different models (nem4-rain, nem4-maxrain, nem4-temp, nem4-maxtemp, prot4-rain, prot4-maxrain, prot4-temp, prot4-maxtemp; Table 4). Because the period of maturation of nematodes

TABLE 4. Description of the population-centered models

Sample size	Response variable	Population-centered model	Explanatory variable
$N = 59$ (701)	Weekly nematode richness of the population	nem4-rain	~ Cumulated rainfall of the week
		nem4-maxrain	~ Maximum rainfall of the week
		nem4-rain2	~ Cumulated rainfall of the past two weeks
		nem4-maxrain2	~ Maximum rainfall of the past two weeks
		nem4-temp	~ Average temperature of the week
		nem4-maxtemp	~ Maximum temperature of the week
		nem4-temp2	~ Average temperature of the past two weeks
		nem4-maxtemp2	~ Maximum temperature of the past two weeks
$N = 67$ (812)	Weekly protozoa richness of the population	prot4-rain	~ Cumulated rainfall of the week
		prot4-maxrain	~ Maximum rainfall of the week
		prot4-rain2	~ Cumulated rainfall of the past two weeks
		prot4-maxrain2	~ Maximum rainfall of the past two weeks
		prot4-temp	~ Average temperature of the week
		prot4-maxtemp	~ Maximum temperature of the week
		prot4-temp2	~ Average temperature of the past two weeks
		prot4-maxtemp2	~ Maximum temperature of the past two weeks

Sample sizes given (N) indicate the number of weeks considered and numbers in parentheses represent the total number of fecal samples considered.

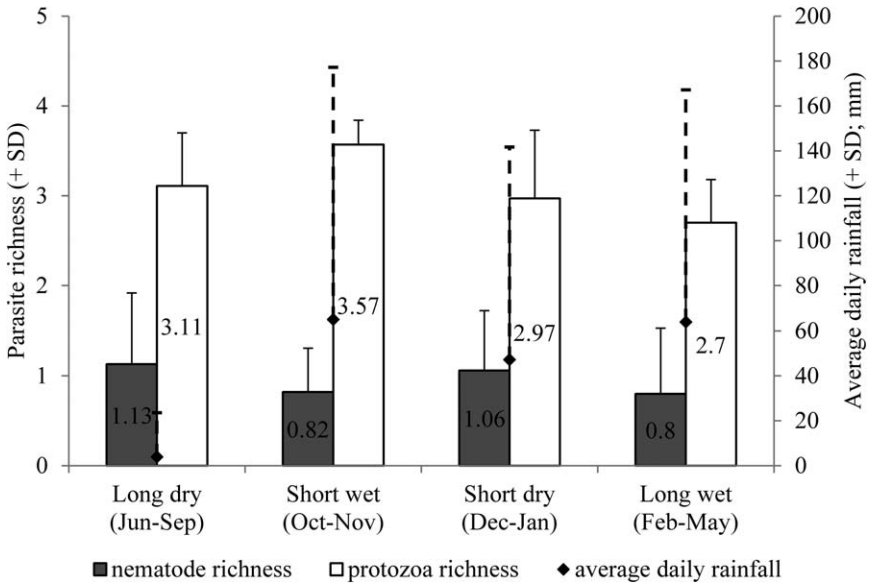

Fig. 1. Seasonal patterns of parasite richness and variations in rainfall. Nematode (grey bars) and protozoa (white bars) richness of the population correspond to the mean number of nematode and protozoa taxa (+SD) for each season on a subset of samples (nematodes; see Methods) or on all collected samples (protozoa). Different years were pooled together because the year of collection had no effect in our models.

is approximately around two weeks depending on species and climatic conditions, we further investigated the effect of past rainfall and temperatures in additional models including the cumulated and maximal rainfalls and the average and maximal temperatures (continuous variables) recorded during two weeks before fecal collection (nem4-rain2, nem4-maxrain2, nem4-temp2, nem4-maxtemp2, prot4-rain2, prot4-maxrain2, prot4-temp2, prot4-maxtemp2; Table 4). Due to obvious correlations, we tested each of these continuous explanatory variables in different models. The year of sample collection was considered as a random effect in all population-centered models. Moreover, in preliminary analyses, we tested for a potential sampling bias by considering the number of individuals sampled per week as an additional fixed factor. As this factor was consistently nonsignificant, we did not keep it in the selected models. We chose the best final models as described above.

Climate data

There are four seasons in Gabon: a long rainy season (Feb–May), a long dry season (Jun–Sept), a short rainy season (Oct–Nov), and a short dry season (Dec–Jan). A weather station (Davis, Vantage Pro2) located in Bakoumba records daily rainfall and temperature (measured every 30 min). Examination of these climatic patterns revealed that the area experienced a marked long dry season (<4 mm of rain per day on average) compared with the three other seasons (60.2 mm of rain per day on average; Fig. 1). Temperatures are also lowest during this long dry season (average temperature = 22.1°C;

TABLE 5. Parasite taxa found in the mandrill population

Parasite phylum	Species (order)	No species	Prevalence (%)
Nematodes	*Necator americanus* (Strongylida)	1	59.7
	Trichostrongylus sp. (Rhabditida)	>1	23.4
	Strongyloides sp. (Rhabditida)	>1	13.9
	Mammomonogamus sp. (Strongylida)	1	2.3
	Enterobius vermicularis (Oxyurida)	1	2.0
Protozoa	*Balantidium coli* (Ciliate)	1	73.8
	Endolimax nana (Amoeba)	1	72.8
	Entamoeba coli (Amoeba)	1	66.4
	Entamoeba histolytica/dispar complex (Amoeba)	2	55.6
	Pseudolimax butschlii (Amoeba)	1	12.2
	Coccidian sp (Apicomplexa)	>1	8.3
	Entamoeba hartmanni (Amoeba)	1	4.7

For each taxa, prevalence is calculated by dividing the number of positive samples by the total number of samples collected over the study period.

range = 15.2–31°C) and highest during the long rainy season (average temperature = 23.8°C; range = 17.8–33.6°C).

Individual traits

We considered the influence of the following individual parameters on parasite richness: sex, dominance rank, age, and female reproductive status.

Dominance rank. Social dominance rank was calculated from dyadic interactions based on daily observations of the mandrills. Interactions between known individuals were scored during ad libitum and focal samplings performed during the study period. We calculated dominance rank by using the outcomes of approach-avoidance interactions. Dominance rank is linear for both males and females but cannot be compared between sexes. Female rank is stable throughout females' lives and inherited from the mother (Setchell et al., 2002). Although rank is linear, some females were less frequently observed than others and it was not possible to define precisely their exact position in the hierarchy. We therefore classified adult females into three different classes of equal size: the first third of females were considered as high-ranking females, the second third as middle-ranking females, and the last third as low-ranking females. In contrast to females, male rank changes over time. A monthly dominance rank was therefore attributed to the studied males. We also defined three classes of ranks. The alpha male was considered the only high-ranking male, the next three males in the hierarchy were considered middle-ranking males and all other males were considered low-ranking males. Some months, two dominant males were very close in the hierarchy and alternatively occupied the first or second rank. At this specific time, we considered both males as high-ranking males. We only evaluated the rank of males aged five years and older. Indeed, juvenile and young adolescent males follow their mother's rank before acquiring their own rank, which is first age-dependent and then linked to the male's competitive abilities. Adolescent males are therefore usually of low-rank and age and rank are not independent.

Age. Exact birth dates of captive-born individuals were known thanks to daily demographic monitoring at CIRMF (Setchell et al., 2002). The exact age of wild-born individuals was known for individuals born after the beginning of the Mandrillus Project. The age of older wild-born animals was estimated using general body condition and, for some individuals, using patterns of tooth eruption and wear (Galbany et al., 2014).

Female reproductive status. In this population, most births occurred between December and February, with a second, smaller birth peak in April-May (MJEC, unpublished data). We evaluated the menstrual cycle of mature females by visual inspection of their sexual swellings: females were considered cycling when they presented an edematous skin involving the vulval, pubic and circumanal regions (Dixson, 1983). Gestation was further deduced from patterns of birth and by the presence of a particular pink tumescence (Setchell et al., 2002). We distinguished three "trimesters" of gestation: the first period spanned from day 1 to day 58 (G1), the second period spanned from day 59 to day 116 (G2), the third period spanned from day 117 to birth (G3). For each female, we recorded the proportion of time spent in tumescence, in gestation, and in lactation per month (number of days in a particular reproductive phase divided by the total number of days). Finally, for gestating females, we considered the proportion of time spent in the first period of gestation vs. in the second/third period of gestation, grouped together because of limited sample sizes.

RESULTS

We found that free-ranging mandrills were infected with 12 different parasite taxa (five nematodes and seven protozoa; Table 5). Over the study period, individual hosts were, on average, infected with 0.92 ± 0.81 (mean $\pm$ SD) nematode taxa and 2.94 ± 1.17 protozoa taxa (Table 5).

Individual-centered models

All individuals. Individual-centered models performed on all studied hosts revealed distinct seasonal patterns of nematode and protozoa richness (nem1a and prot1a; Table 6; Fig. 1). Individuals harbored more nematode species during the long dry season than during the long rainy season (intercept with long dry season as the reference = 1.57; long rainy season: estimate = -0.26, $P = 0.04$, d$f = 61$), but harbored more protozoa

TABLE 6. Results of the individual-centered models

Considered individuals	Individual-centered model	Explanatory variable	d*f*	Estimate	*F* value	*P*
(a) Nematode richness						
All individuals	nem1a	Season	3		2.99	0.04
		Age	1	−0.04	10.33	<0.01
	nem1b-rain	Rainfall	1	−1.54e-04	13.22	<0.001
		Age	1	−0.04	9.47	<0.01
	nem1b-temp	Temperature	1	−0.14	10.86	<0.01
		Age	1	−0.04	10.53	<0.01
Mature males	nem2a	Season	3		0.48	>0.1
Mature females	nem3a	Season	3		2.10	>0.1
	nem3b-rain	Rainfall	1	−1.98e-04	8.68	<0.01
	nem3b-temp	Temperature	1	−0.16	6.22	0.02
(b) Protozoa richness						
All individuals	prot1a	Season	3		7.06	<0.001
	prot1b-rain	Rainfall	1	2.75e-05	0.14	>0.1
	prot1b-temp	Temperature	1	−0.02	0.08	>0.1
Mature males	prot2a	Season	3		2.81	0.04
	prot2b-rain	Rainfall	1	2.76e-05	0.05	>0.1
	prot2b-temp	Temperature	1	−0.07	0.27	>0.1
Mature females	prot3a	Season	3		4.03	0.01
	prot3b-G	Gestation	1	0.51	7.45	<0.01
	prot3b-L	Lactation	1	−0.44	4.20	0.05
	prot3b-T	Tumescence	1	0.01	0.003	>0.1
	prot3b-G1	G1	1	0.69	9.23	<0.01
	prot3b-G2-3	G2-3	1	0.12	0.16	>0.1
	prot3c-G	Gestation	1	0.81	16.19	<0.001
	prot3c-G1	G1	1	0.66	7.48	0.01

Selected models are presented only (i.e., with an AIC at least two units lower than the second best alternative model).

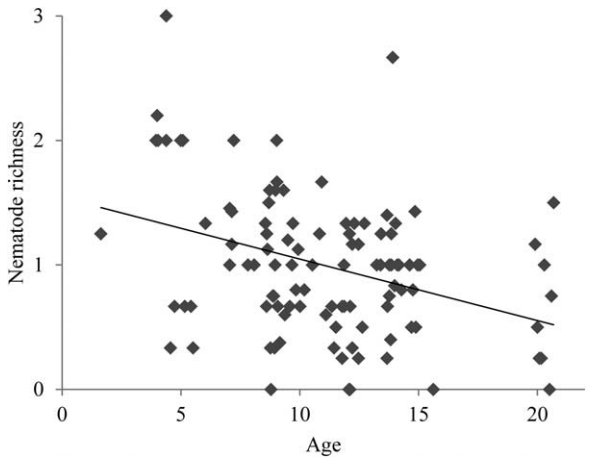

Fig. 2. Effect of age on nematode richness. Each data point represents monthly average individual nematode richness as a function of individual age.

species during the short rainy season compared with the three other seasons (intercept with short rainy season as the reference = 3.54; long dry season: estimate = −0.46, $P < 0.01$, df = 77; short dry season: estimate = −0.61, $P = 0.01$, df = 77; long rainy season: estimate = −0.88, $P < 0.001$, df = 77). While sex had no effect on richness in both nematodes and protozoa, nematode richness specifically was significantly higher in young individuals than in old individuals [nem1a; Table 6, (a); Fig. 2]. We further found contrasting results concerning climatic factors: nematode richness specifically decreased with rainfall and average temperature [nem1b-rain and nem1b-temp; Table 6, (a)].

Males. In males, neither age nor dominance rank significantly influenced richness in nematodes and protozoa (nem2a and prot2a; Table 6). Season influenced protozoa richness [prot2a; Table 6, (b)] but this effect did not result from rainfall or temperature patterns [prot2b-rain and prot2b-temp; Table 6, (b)].

Females. Similarly to males, in females, neither age nor dominance rank affected nematode or protozoa richness (nem3a and prot3a; Table 6). There was no overall effect of season on nematode richness [nem3a; Table 6, (a)], although two-by-two comparisons revealed that the latter was higher during the long dry season than during the long rainy season (intercept with long dry season as the reference = 1.06; long rainy season: estimate = −0.40, $P = 0.02$, df = 35). This effect is likely due to climatic patterns, because nematode richness also decreased with rainfall and average temperature and was not influenced by any of the variables linked to female reproductive status [nem3b-rain and nem3b-temp; Table 6, (a)]. In contrast, females harbored more protozoa species during the short rainy season than during the long dry and long rainy seasons [prot3a; Table 6, (b); intercept with short rainy season as the reference = 3.55; long dry season: estimate = −0.51, $P = 0.03$, df = 44; long rainy season: estimate = −0.90, $P = 0.001$, df = 44]. However, the seasonal variations of richness in protozoa were not due to climatic conditions [prot3b; Table 6, (b)] but were rather linked to female reproductive status: gestating females were parasitized by more protozoa species than non-gestating females [prot3b-G; Table 6, (b); Fig. 3]. Moreover, protozoa richness was found to be higher in early gestating females than in other gestating females [prot3b-G1; Table 6, (b)]. To confirm that this gestational effect was not due to

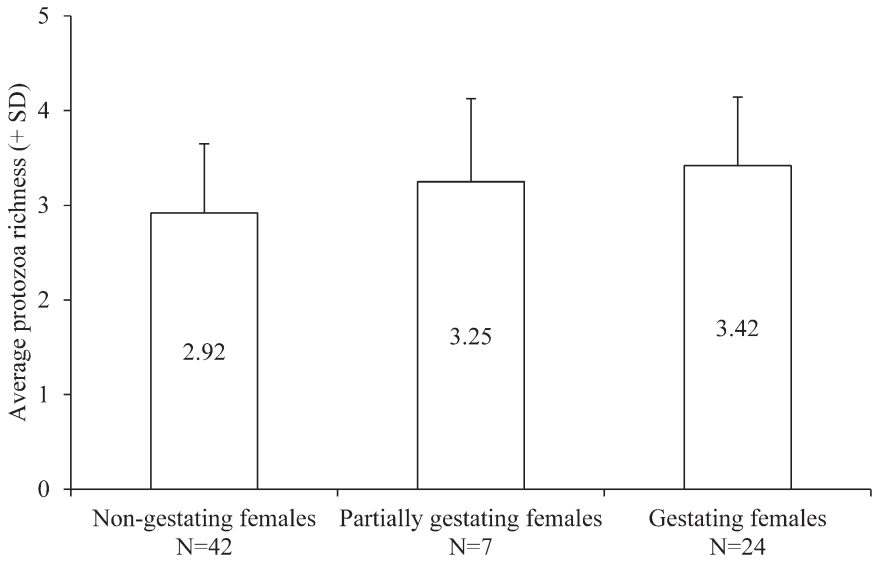

Fig. 3. Effect of protozoa richness on female reproductive status. Monthly average protozoa richness (+SD) are calculated for non-gestating females, partially gestating females and gestating females (as defined in the Methods). Sample sizes correspond to the number of lines of data considered (see Methods).

TABLE 7. Results of the population-centered models for nematode richness

Explanatory variable	d*f*	Estimate	*F*-value	*P*
Cumulated rainfall of the week	1	−1.97e-4	1.19	0.10
Maximum rainfall of the week	1	−1.21e-3	2.67	0.10
Cumulated rainfall of the past two weeks	1	−2.23e-4	5.03	<0.05
Maximum rainfall of the past two weeks	1	−1.63e-3	6.80	0.01
Average temperature of the week	1	−0.10	4.37	<0.05
Maximum temperature of the week	1	−0.10	3.85	0.05
Average temperature of the past two weeks	1	−0.07	4.01	0.05
Maximum temperature of the past two weeks	1	−0.06	3.60	0.07

Selected models are presented only (i.e., with an AIC at least two units lower than the second best alternative model).

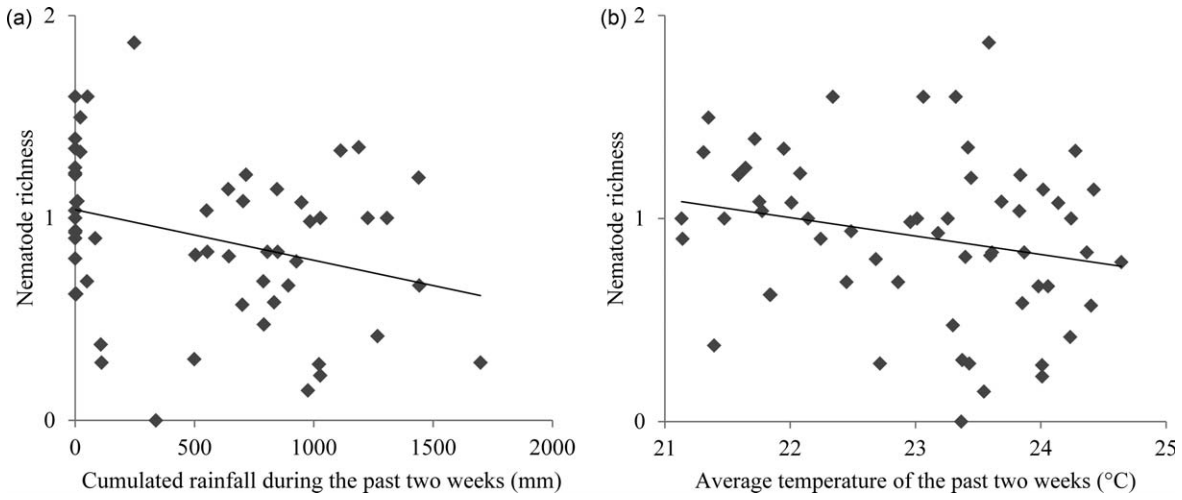

Fig. 4. Effect of weather conditions of the past two weeks on nematode richness. Each data point represents weekly average nematode richness recorded in the population as a function of (**a**) cumulated rainfall recorded during the past two weeks; (**b**) average temperature recorded during the past two weeks.

confounding effects of the season, we restricted our dataset to the months where the proportion of G1 females was the highest (i.e., the late long dry and the short rainy seasons: 16 females, $N = 34$ lines of data for protozoa, mean ± SD: 4.47 ± 1.52 samples/female/month, representing 152 fecal samples). We found the same strong effect of time spent in gestation, particularly in G1 [prot3c-G and prot3c-G1; Table 6, (b)], on protozoa richness. Furthermore, lactating females tended to harbor fewer protozoa species than non-lactating females, although this result only approached significance (prot3b-L). Finally, we did not find any evidence that time spent in tumescence impacted protozoa richness [prot3b-T; Table 6, (b)].

Population-centered models

Cumulated and maximal rainfalls recorded during the 2 weeks before collection negatively impacted nematode richness (Table 7; Fig. 4). Nematodes also tended to decrease with both the maximum and average temperatures of the week and of the two weeks before collection (Table 7; Fig. 4). In contrast, none of the climatic variables had an effect on protozoa richness.

DISCUSSION

We found a combination of environmental and individual effects on the richness of both nematodes and protozoa. Determinants of parasitism in hosts largely depend on the biology of their parasites (Vitone et al., 2004). The distinction we made here between nematodes and protozoa appeared relevant, as we obtained contrasting results regarding these two types of parasites.

Seasonal patterns

Richness in nematodes and protozoa show strong but contrasting seasonal patterns. Nematode richness is the lowest during rainy seasons, while we generally observe the opposite pattern regarding protozoa richness. In accordance with our predictions (H1; Table 1), nematode richness relies on environmental conditions but in an unexpected way, as both rainfall and temperature patterns negatively impact nematode richness in all performed models, while in other primates, humid conditions generally promote parasite richness or abundance (Table 1). Moreover, comparative studies consistently found higher parasite prevalence in primate populations inhabiting more humid environments (McGrew et al., 1989; Stuart et al., 1993). In accordance with our results, however, *Strongyloides* sp. are more likely to occur during the dry season than during the rainy season in wild white-faced capuchins living in a seasonally dry forest, because at this time of the year, capuchins descend to the forest floor to drink from terrestrial sources, where they face contamination (Parr et al., 2013). Equatorial rainforests, where mandrills live, present moist conditions year-round, even during the long dry season, as the average weekly humidity never went below 81% during the study period. In such an environment, humidity is not a limiting factor constraining parasite development. In contrast, significant rainfall could decrease fecal contamination due to "wash-out" effects on free-living stages of nematodes released into the environment. Our population-centered models are in line with this possible mechanism. Indeed, only rainfall recorded two weeks before fecal collection, corresponding to the average maturation time of nematodes in the environment (Neveu-Lemaire, 1952), negatively impact nematode richness. Accordingly, a study on yellow baboons found an attenuation of nematode contamination in the soil during the wet season (Hausfater and Meade, 1982). In contrast, in a captive population of mandrills experiencing similar climatic conditions, nematode prevalence is the highest during the rainy season (Setchell et al., 2007). We suspect that rainfall may not have the same impact on free-living stages of nematodes in captivity as in natural environments. Indeed, in captivity, individuals live year-round in the same restricted area of a few hectares, where contamination risks are high. In the studied population, mandrills travel on average 2.4 km/day (Brockmeyer et al., 2015) and tend not to stay in the same area for several consecutive days (MJEC, unpublished data). When they return to an area that has been visited earlier during the rainy season, rainfall may have cleared up the site. A similar wash-out effect has been proposed to explain seasonal variation of movement patterns in white-eyelid mangabeys *Cercocebus albigena* (Freeland, 1980). The additional negative relationships we found between high temperatures and nematode richness at both the individual and the population levels suggest that free-living stages of nematodes may suffer from desiccation when temperature is high, but this effect generally occurs in dry conditions (Hausfater and Meade, 1982) and not in humid conditions as found in our study. Therefore, the weak patterns observed regarding temperature might likely result from a confounding effect of rainfall because these two climatic variables are highly collinear.

According to our predictions (H1; Table 1), none of the factors linked to climatic conditions have an impact on protozoa richness. In line with our hypothesis too (H3; Table 1), in sexually mature females, the seasonal variation observed in protozoa richness is instead linked to female reproductive status. Indeed, early gestating females harbor more protozoa species than all other females. Previous studies demonstrated a relationship between female reproductive status and parasite richness, although these results generally concerned nematodes and not protozoa. For example, cycling female yellow baboons excrete higher number of nematode eggs than anestrous or pregnant females (Hausfater and Watson, 1976). Nematode egg intensity was also found to be higher in pregnant captive female mandrills than in lactating or cycling females (Setchell et al., 2007). In this latter study though, and unlike our analyses, the confounding effect of the season was not taken into account. The particular hormonal status of pregnant females seems to create unique immunological conditions (Mor and Cardenas, 2010). In livestock, hormones released during gestation can impact nematode parasitism (Dunsmore, 1971; Falzon et al., 2013). In placental mammals, progesterone plays a role by down-regulating cell-mediated immunity in gestating females to increase immune tolerance towards the fetus (Rolland et al., 1978; Clemens et al., 1979; Weinberg, 1987). This pattern is also well described in humans (Mor and Cardenas, 2010). For instance, in regions where malaria occurs, early pregnant women are more susceptible to malaria infections. Higher parasite susceptibility is also reported in the literature during the period around birth, a phenomenon known as the "periparturient rise" (Cattadori et al., 2005; Altizer et al., 2006). This rise is observed in

pregnant Japanese macaques, which harbor a higher nematode prevalence than nonpregnant females (MacIntosh et al., 2010). In contrast, in our study, we do not observe gestational effects on nematode richness, certainly because of a strong wash-out effect observed during the short rainy season that corresponds to the period with the highest proportion of early gestating females. We further were unable to test for a periparturient effect because of the limited sample size in G3. However, an immune-suppressive effect during gestation in mandrills could explain the fact that early gestating females harbor more protozoa than females in other reproductive states. Interestingly, males aged 5 years and older also show similar, but milder, seasonal fluctuations in protozoa richness, independently of climatic conditions. While this latter result could be linked to any environmental parameters that vary with season, if early gestating females are more susceptible to parasites, parasite pressure may increase in the whole population during the short rainy season. Long-term monitoring in combination with hormone analyses are now needed to uncover the physiological mechanisms underlying the relationship between parasitism and gestational status.

Social and demographic variables

We found that young individuals harbor more nematode species than old animals (H5b; Table 1). Previous studies showed that the relationship between age and parasitism is complex and mixed results have been found so far (Table 1). Mandrills may acquire some degree of immunity towards nematodes with age, possibly explaining the lower richness observed in old animals. Indeed, acquired immunity is a trade-off between the costs imposed by such a response and the risks linked to infection. Although often asymptomatic, helminthiasis is responsible for severe disorders in several species, including primates, by causing diarrhea, inflammation, blood loss, anemia or sleeping disturbances (Miller 1968; Prociv and Croese, 1996; Kucik et al., 2004). However, only a few studies in the wild found such an age-infection profile (Müller-Graf et al., 1996; MacIntosh et al., 2012) and immunity against parasites rather results in a convex relationship, including a period with a positive age-infection profile in juveniles followed by a decrease of parasite infections in older individuals (Benavides et al., 2012). The relationship observed for nematode richness could be alternatively explained by a higher exposure of juveniles to infective parasite stages in the environment, as suggested for juvenile Japanese macaques infected with *Strongyloïdes fuelleborni* (MacIntosh et al., 2010).

Because of inequities in immunity between sexes and dominance ranks, both factors have been proposed to influence parasite population dynamics in several mammalian species (Table 1). In contrast with our predictions (H2 and H4; Table 1), neither sex nor dominance rank impact parasite richness. These results are in line with those found in other primate species (sex: captive mandrills (Setchell et al., 2007), eastern chimpanzees (Gillespie et al., 2010), white-faced capuchins (Parr et al., 2013); dominance rank: chacma baboons (Benavides et al., 2012), white-faced capuchins (Parr et al., 2013), red-fronted lemurs (Clough et al., 2010), eastern chimpanzees (Muehlenbein and Watts, 2010)). Such discrepancies between species presumably result from different biological mechanisms and are therefore difficult to explain. However, we cannot exclude that in mandrills, other estimates such as parasite abundance, may depend on host sex or on dominance rank. More studies are therefore necessary to improve our understanding of the complex role of social and demographic determinants on parasitism in this species and other non-human primates.

In conclusion, we showed that a range of factors determine gastrointestinal parasitism in wild mandrills. There are contrasted biological mechanisms underlying the seasonal patterns observed for nematodes and protozoa. These results emphasize the necessity to consider the ecological context as well as the biology of the examined parasites when attempting to identify infection risks. Longitudinal monitoring of wild populations using individually-centered approaches is necessary to unravel the complexity of parasite population dynamics and to estimate the detrimental effects of parasites on endangered species.

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