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## Costs and drivers of helminth parasite infection in wild female baboons

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## ABSTRACT

1. Helminth parasites can have wide ranging, detrimental effects on host reproduction and survival. These effects are best documented in humans and domestic animals, while only a few studies in wild mammals have identified both the forces that drive helminth infection risk and their costs to individual fitness.
2. Working in a well-studied population of wild baboons (*Papio cynocephalus*) in the Amboseli ecosystem in Kenya, we pursued two goals, to: (i) examine the costs of helminth infections in terms of female fertility and glucocorticoid hormone levels, and (ii) test how processes operating at multiple scales—from individual hosts to social groups and the population at large—work together to predict variation in female infection risk.
3. To accomplish these goals, we measured helminth parasite burdens in 745 fecal samples collected over 5 years from 122 female baboons. We combine these data with detailed observations of host environments, social behaviors, hormone levels, and interbirth intervals.
4. We found that helminths are costly to female fertility: females infected with more diverse parasite communities (i.e. higher parasite richness), exhibited longer interbirth intervals than females infected by fewer parasite taxa. We also found that females exhibiting high *Trichuris trichiura* egg counts also had high glucocorticoid levels. Female infection risk was best predicted by factors at the host-, social group-, and population level: females facing the highest risk were old, socially isolated, living in dry conditions, and infected with other helminths.
5. Our results provide an unusually holistic understanding of the factors that contribute to inter-individual differences in parasite infection, and they contribute to just a handful of studies linking helminths to host fitness in wild mammals.

**Key-words:** baboons, fitness costs, female fertility, glucocorticoid hormones, helminth infection, *Trichuris trichiura*, primates

## 1. INTRODUCTION

In humans and domestic animals, the costs of helminth parasitism are well known, with wide-ranging effects on host growth, reproduction, mortality, and susceptibility to other parasites (Bethony et al., 2006; Charlier et al., 2014; Hotez et al., 2008). However, studies that link the costs of helminth parasitism to components of host fitness in natural populations, especially wild non-human primates, are rare (e.g. Nguyen et al., 2015). This gap exists despite the fact that documenting the natural costs and drivers of helminth infection is valuable to reveal the selection pressures that shape mammalian behavior and life histories, identify individuals that are most at risk, and inform management strategies in vulnerable populations (Kaur and Singh, 2009; Tompkins and Begon, 1999).

Gastrointestinal helminths impose both direct and indirect costs on hosts. Direct costs result from competition for resources required by both the helminth and its host (e.g. red blood cells), or from pathological damage to the host's intestine that interferes with absorption of important nutrients required to support and fight infection (Graham, 2008; Pedersen and Fenton, 2007). Indirect costs occur when hosts reallocate energetic resources to fight helminth infections at the expense of other costly activities, such as survival and reproduction (Crompton and Nesheim, 2002; Koski and Scott, 2001). With regard to reproductive costs, female mammals make large energetic investments in gestation and lactation, which might be constrained by helminth infection (Khokhlova et al., 2002; McFalls et al., 1984). In support, the experimental removal of ecto- and endoparasites sometimes leads to increased reproductive success (Hillegass et al., 2010; Neuhaus, 2003; Patterson and Ruckstuhl, 2013, but see Gooderham and Schulte-Hostedde, 2011; Raveh et al., 2015, 2011). In primates, previous research by Nguyen et al. (2015) found that female gelada baboons infected by *Taenia* species exhibit longer interbirth intervals (a measure of fertility) than those not infected. In humans, Blackwell et al., (2015) find contrasting relationships between helminths and female fertility; roundworm infection is associated with early age at

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first birth and short interbirth intervals, whereas infection with hookworm is associated with late age at first pregnancy and long interbirth intervals.

The physiological costs associated with helminth infection may be reflected in hormones that indicate host energetic expenditure, such as glucocorticoids (GCs). Several studies, both experimental and observational in the wild, have found significant positive correlations between host GC levels and patterns of helminth infection (Friant et al., 2016; Michael P. Muehlenbein and Watts, 2010; Müller-Klein et al., 2018; Sures et al., 2001). However, some studies find no predictable relationships between parasites and host GCs, perhaps due to host tolerance, or the fact that some parasites have only minor effects on host energy reserves, or that different parasites elicit different responses from the immune-endocrine system (Goldstein et al., 2005; Monello et al., 2010). These apparently contradictory results probably reflect the complex nature of potential relationships between host physiology and parasite infection. For instance, host GC levels may rise in response to the energetic stress imposed by parasite depletion of host resources (Coop and Kyriazakis, 1999). GCs may also rise in response to activation of the immune system by helminth infections. Specifically, GCs exert anti-inflammatory and immunosuppressive effects by inhibiting the secretion of interleukin-1 (IL-1), which regulates the T-helper 2 system important for clearing helminth infections (Helmbj and Grencis, 2004; Lee et al., 1988). Importantly, the immunosuppressive effects of GCs may also underlie relationships between GCs and parasitism; if elevated, GCs might reduce host resistance to infection leading to a positive relationship between GCs and helminths. On the other hand, GCs and helminths may be negatively correlated, if, for instance, females in good physical condition invest heavily in reproduction; in this case, females might exhibit high GCs and low parasite burdens because they have the resources to do both (reproduce and fight parasites).

In addition to investigating potential costs of infection, we sought to understand the patterns and drivers of individual infection risk. Doing so can help uncover the adaptive value of behavioral strategies and social structures, and point to selection pressures and

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constraints that have shaped mammalian behavior and life history. Infection risk is defined as the probability that a host acquires an infection. Variation in individual infection risk is thought to be largely reflected in existing patterns of infection in natural populations. In group-living animals, the drivers of infection risk can be categorized into three main hierarchical processes: those operating at the level of individual hosts, social groups, and the host population at large (see Fig. 1 for examples of these hierarchical processes in female baboons). These processes act through two broad mechanisms to ensure successful infection of hosts and subsequent transmission of helminth infectious stages to additional hosts: (1) host exposure to helminth infectious stages, and (2) host susceptibility, including the host's quantitative resistance to helminth infection (i.e., the ability to limit parasite burden once a host is exposed and infected).

Disentangling the causal links between exposure, susceptibility, and parasite burdens is challenging, and often impossible, in observational studies. What is possible is to draw inferences about the drivers of individual variation in infection risk by correlating infection patterns with host-, group-, and population-level traits. At the host-level, traits such as age, reproductive state, sex, body mass, social connectedness, and social status (i.e., dominance rank) all influence helminth exposure and susceptibility. In support, many studies of wild female mammals find that individuals who are older, pregnant or lactating, large bodied, and socially connected exhibit the highest parasite burdens (Foo et al., 2017; Nunn and Altizer, 2006; Rushmore et al., 2017; Vitone et al., 2004; Wilson et al., 2002; Zuk and McKean, 1996). At the group-level, factors such as group size and home range use also shape parasite exposure and susceptibility. For instance, individuals living in large groups at high densities face both intense resource competition and high parasite exposure, which can lead to high helminth burdens (Cote & Poulin, 1995; Kappeler, Cremer, & Nunn, 2015; Rifkin et al., 2012). Population-processes such as rainfall and temperature may determine the survival of parasite infectious stages in the environment, host physical condition, and host behavior, all of which have consequences for parasite exposure and susceptibility (Nunn

and Altizer, 2006). Finally, co-infection by multiple parasite species can also shape infection risk, driven by both host- and population-level processes. At the host level, different parasite species may facilitate or inhibit each other's proliferation and transmission through resource competition or immune mediated interactions (Graham, 2008; Jolles et al., 2008; Pedersen and Fenton, 2007) At the population level, helminths that thrive in similar environmental conditions (e.g. humidity, temperature) may co-occur in hosts because hosts are more likely to be exposed to these parasites at the same time.

In this study, we leveraged long-term data on wild female baboons in Kenya to understand costs linked to a diverse community of helminth parasites and test how processes occurring at multiple scales—from hosts, to social groups, and the host population—influence helminth infection risk. Female baboons are useful for understanding the reproductive costs of parasitism because they reproduce year-round and, unlike most mammals, they exhibit obvious external signs of their reproductive state, including ovarian cycling, pregnancy, and postpartum amenorrhea (Beehner et al., 2006; Gesquiere et al., 2007). The Amboseli ecosystem is highly seasonal, with distinct wet and dry seasons that have likely consequences for both helminth survival and baboon condition. Baboons live in multi-male, multi-female social groups, and females' social lives are governed by linear dominance hierarchies and complex grooming networks, which predict social support (Silk et al., 2010). Because female baboons are matrilineal, the Amboseli baboon project can follow their lives from birth, providing exact information on individual age—information that is often not available for wild animal populations.

Our specific objectives were to: (1) identify the costs of helminth infection on female baboons, as evidenced by links to measures of female fertility and glucocorticoid hormones, and (2) test how host-, group-, and population-level processes predict female infection risk. For the first objective, we used female interbirth intervals (IBIs) as our primary measure of female fertility because IBIs reflect the rate at which females produce offspring. We tested the relationships between parasitism and IBI duration, as well as each of the IBI's

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component phases: postpartum amenorrhea (PPA), sexual cycling, and pregnancy. In general, we expected that higher parasite burdens would be associated with longer IBIs and component phases because female condition and energy reserves influence female readiness for reproduction (Gesquiere et al., 2018). However, these predictions primarily apply to PPA and sexual cycling; the predictions for pregnancy are less clear. Pregnancy is relatively invariant in this and other primate populations (Gesquiere et al., 2018), and while parasites might lengthen pregnancy, we might also expect high parasite burdens to be linked to short gestations because poor maternal body condition can lead to premature birth (Ellison, 2003).

With respect to glucocorticoids, we predicted that higher helminth burdens would be associated with elevated GCs, either because GCs reflect the costs of fighting infection or because GCs are immunosuppressive, or both. However, if elevated GCs indicate high reproductive investment arising from high phenotypic quality, we might observe a negative relationship between GCs and helminths.

For the second objective, our specific predictions for how host-, group-, and population-level traits might be related to female infection risk are described in Figure 1. Together, our multi-scale perspective on both the costs and predictors of parasitism in female baboons provides an unusually holistic understanding of the causes and consequences of helminth infection in a wild primate.

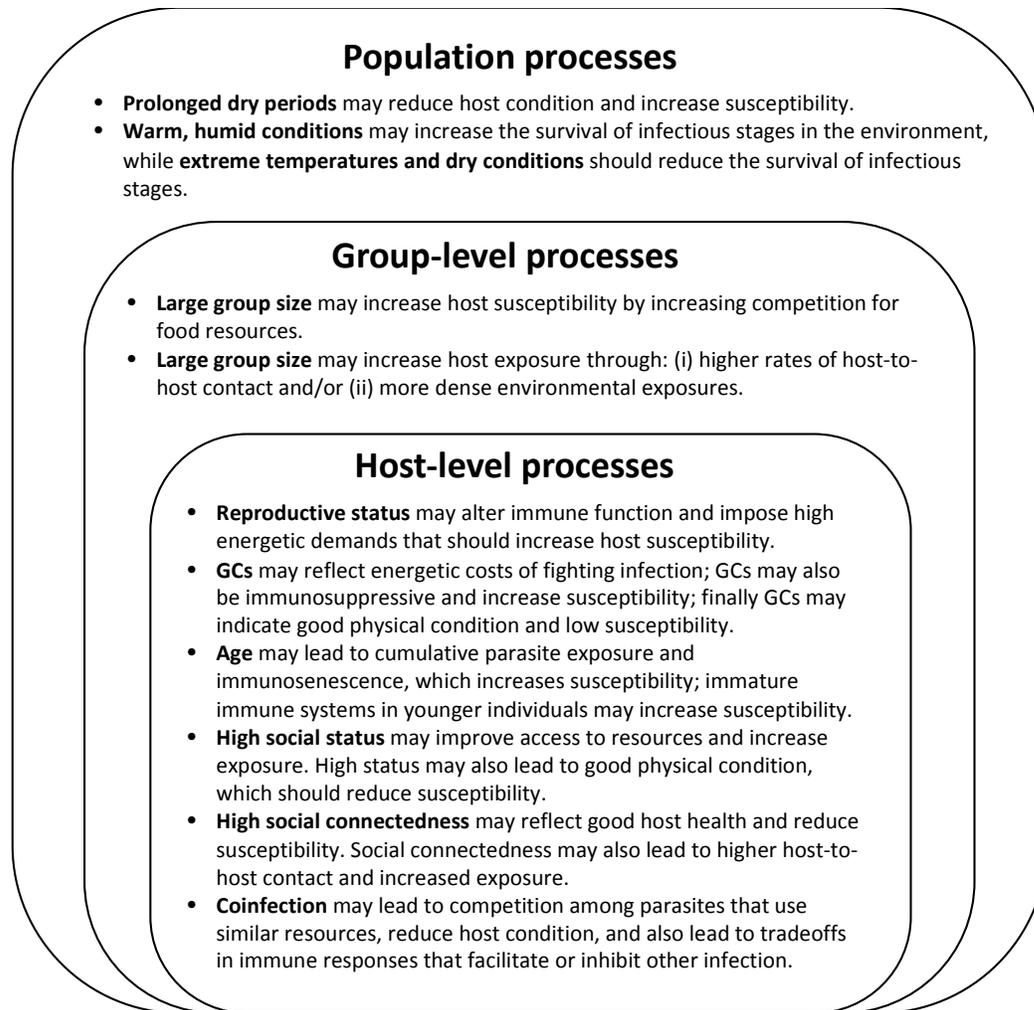


Fig 1. Processes proposed to drive inter-host variation in helminth infection risk in female savannah baboons. These processes operate at the level of the host population, host social groups, and individual hosts, as indicated by the concentric circles. See main text and Table S1 for key citations regarding these processes.

## 2. MATERIALS AND METHODS

### 2.1 Study population and site

The Amboseli ecosystem in Kenya ( $2^{\circ}40'S$ ,  $37^{\circ}15'E$ , 1100m) is a semi-arid short-grass savannah that is home to a population of wild baboons monitored by the Amboseli Baboon Research Project (ABRP) (Alberts and Altmann, 2012; Alberts et al., 2005).

Observers collect behavioral, environmental, and demographic data on the members of 4 to 6 study groups at any given time; each study group is monitored 2-4 days each week

(Alberts and Altmann, 2012). Because multiple permanent group fissions occurred during the study period –March 2011 and September 2015 – the data in this study came from a total of 13 different social groups. All data collection procedures adhered to the regulations of the Institutional Animal Care and Use Committee of Duke and Notre Dame Universities, and the laws of Kenya.

## 2.2 Fecal sample collection and parasitology

Fecal samples (n = 745) were collected opportunistically from 122 adult females during the course of normal monitoring (mean = 6.11; range = 1-25 samples per individual). Samples were collected within a few minutes of defecation. Each sample was homogenized and stored in 10% buffered formalin. Helminth egg counts were performed using standard floatation and sedimentation protocols adapted from Gillespie (2006) (see Supplementary Methods for a detailed description). We identified 9 parasite taxa across all samples. However, in our analyses of parasite risk, we focused on the four most prevalent parasites (*Trichuris trichiura*, strongyles, *Abbreviata caucasica*, and *Streptopharagus pigmentatus*), as well as parasite richness (i.e. the number of distinct parasite taxa in each sample). Note that the term “strongyle” refers to all parasites belonging to the family Strongylidae, which are known to be morphologically similar; hence, this category likely includes multiple helminth species.

We describe how other required data sets were collected, including the duration of interbirth intervals in Section 2.3; we discuss fecal glucocorticoid concentrations in Section 2.4, and other host, group, and population drivers of parasitism in Section 2.5. We then describe how sample-specific parasite data were used as predictors of female fertility in Section 3.1, and as predictors of fecal GC concentrations in Section 3.2. Finally, in Section 3.3 we describe our modeling of parasite data as response variables in our analyses of multi-scale predictors of female parasite risk.

### **2.3 Measuring female interbirth intervals**

We used female interbirth intervals (IBIs) as a measure of female fertility. To measure IBIs and their component phases— postpartum amenorrhea (PPA), sexual cycling, and pregnancy—ABRP collects continuous, individual-based data on female sexual swellings, color changes to the paracallosal skin, and menstrual bleeding, allowing us to track female reproductive state with high accuracy (Beehner et al., 2006; Fitzpatrick et al., 2014; Gesquiere et al., 2007). We measured IBI durations using the same methods as Gesquiere et al. (2018), which conducted a comprehensive analysis of interbirth intervals in our population. Specifically, we measured IBI duration in days between two successive live births, where the first infant survived for at least 1 year. We imposed this restriction because, like many mammals, when female baboons lose an infant, they rapidly return to ovarian cycling, leading to a greatly truncated IBI. The duration of PPA was defined as the number of days from the birth of an infant who survived at least 1 year to the onset of swelling in the first sexual cycle following the infant's birth. The duration of sexual cycling was the number of days from the onset of swelling in the first cycle after PPA to the onset of deturgescence during the conceptive cycle that led to the birth of a live offspring. The duration of pregnancy was the number of days from the first day of deturgescence during the conceptive cycle to the birth of a live offspring.

### **2.4 Measuring fecal glucocorticoid concentrations**

To test whether parasites impose costs that are reflected in female glucocorticoid levels, we measured fecal glucocorticoid (fGC) concentrations in 702 of the 745 fecal samples where we had also measured parasitism (mean = 5.75 samples per individual; range = 1-24 samples). Briefly, fecal samples were preserved in 95% ethanol and stored in an evaporative cooling structure in Amboseli until transport to the laboratory in Nairobi, where they were freeze dried, sifted to remove large vegetative matter, and weighed. The weighed fecal powder (0.2g) underwent extraction in 90% methanol, followed by solid phase extraction using Waters Oasis HLB cartridges. Fecal GC (fGC) metabolites in the samples

were measured in ng per g of dried feces by radio-immunoassays (RIA), following a well-established protocol (e.g. Gesquiere et al., 2011, 2008; Markham et al., 2015; Onyango et al., 2008). We used the Corticosterone kit for Rats and Mice (ICN diagnostics, Costa Mesa, CA) which has previously been validated for our population (Gesquiere et al., 2005; Khan et al., 2002; Lynch et al., 2003). Full protocols for measuring fGCs are available for download at <http://amboselibaboons.nd.edu/downloads/>.

## 2.5 Measuring predictors of parasite infection

To test multi-scale predictors of female parasitism, we also required data on several factors that varied across individual hosts, social groups, and over time in the population.

*Host level predictors.* Age on the day of fecal sample collection was known within a few days and modeled as a continuous variable. Age is known because females are born into our study groups and remain in their natal group (or one of its fission products) throughout their lives. The age range of our study subjects was 4.25 years to 25.45 years (mean = 12.61 years).

*Female reproductive state.* Whether a female was cycling, pregnant, or in postpartum amenorrhea on the day of fecal sample collection was known using the signs of female reproductive states described in Section 2.3.

*Fecal glucocorticoid (fGC) concentrations* may be immunosuppressive, and as such, they may play a dual role as both a potential predictor of and a potential response to helminth burdens (Sapolsky et al., 2000). Hence, in addition to testing whether parasite burdens predicted GCs, we also included fGC concentrations (measured in the same fecal sample where we also characterized parasite burdens) in our multivariate analyses of parasite infection risk.

*Dominance rank* in the month of sample collection was measured by calculating ordinal dominance ranks based on observed dyadic agonistic encounters (Hausfater, 1975). Ranks are assigned monthly to each individual in each study group. The highest ordinal rank is 1, the second rank is 2, and so on. Female dominance ranks are kin-based and stable

over time; dominance rank in the month of sample collection is tightly correlated with female rank over longer time periods ( i.e. 1 year or multiple years; Samuels et al., 1987).

*Social connectedness* to adult females and adult males was calculated over the year prior to sample collection using a previously developed metric that quantifies the frequency in which each female gave or received grooming to/from adult females or males, relative to all the other females alive in the population at the same time (Archie *et al.* 2014). We calculated social connectedness over a 1-year period because this duration optimized the resolution in the data in prior analyses (Archie *et al.* 2014). Positive values indicate females who groom more than other females; negative values are those who groom less than other females.

Group-level predictor. *Group size* was calculated as the total number of individuals in the female's group on the day of sample collection. Group size was modeled as a continuous variable and is known from near-daily censuses of all the members of each social group.

Population-level predictors. Amboseli experiences a dry season between June-October, and a wet season between November-May (Gesquiere *et al.* 2011a). Rainfall is highly variable, ranging from 150-750 mm/year, with a mean of 344 mm/year (Alberts et al., 2005; Altmann et al., 2002). Temperatures ranged between 28°C and 35°C (mean = 32.30°C). We modeled climate variables using *total rainfall* and *average maximum daily temperature* in the three months prior to sample collection. We chose a 3-month period for two reasons: (1) we speculated that 3 months was a good estimate of environmental conditions influencing host body condition (e.g. food availability) and the prepatent period between host infection and egg shedding; and (2) a 3-month window best predicted parasite burdens in a sensitivity analysis. Rainfall and temperature data are collected using a rain gauge and min/max thermometer located at the project's field camp.

### 3.0 Statistical analyses

#### 3.1 The costs of helminths: testing if helminth infection is linked to longer IBIs.

We used a mixed modeling approach to test whether measures of helminth burden were linked to measures of female fertility, as measured by female IBIs or their component phases. Here and below, all models below were built in R using the packages *AICcmodavg* (Mazerolle, 2011), *lme4* (Bates et al., 2015), and *lmerTest* (Kuznetsova et al., 2016). We built separate models for each of the four response variables, which were durations in days for: (1) the full IBI ( $N = 116$  IBIs from 77 females), (2) postpartum amenorrhea ( $N = 108$  PPAs from 76 females), (3) ovarian cycling ( $N = 61$  periods of ovarian cycling from 52 females), and (4) pregnancy ( $N = 66$  pregnancies from 49 females). Because female IBI durations are driven by many factors (e.g. age, parity, dominance rank), we began by recreating models that included all of the significant fixed effects in Gesquiere et al. (2018), a recent, comprehensive study of the predictors of IBI variation in our population. Specifically, the IBI model included rank, primiparity, and group size. The PPA model included rank, primiparity, group size, and rainfall. The cycling model included primiparity, and the pregnancy model included rainfall. Importantly, some of these fixed effects were not significant in the models we present here, but because our data set was smaller than in Gesquiere et al. (2018), we retained these fixed effects to account for known predictors of variance.

After including these fixed effects from Gesquiere et al. (2018), we then simultaneously added all five measures of female parasite risk (see below) and then used backwards elimination via the step function in the *lmerTest* package (Kuznetsova et al., 2016), which uses log likelihood ratio tests, to find the best-fitting model. This best-fitting model always retained the fixed effects included by Gesquiere et al. (2018), and had the potential to include none, one, or more than one of the five measures of parasite risk. The five measures of parasite risk were mean parasite egg counts for all fecal samples collected during each IBI or component phase for (1) *Trichuris trichiura* (because these counts were not normal, 1 was added to all counts and log-transformed), (2) strongyles, (3) *Abbreviata*

*caucasica*, (4) *Streptopharagus pigmentatus*, and (5) mean parasite richness as a count of the number of different helminth taxa observed in each fecal sample. Our sample sizes for these analyses (Table 1) included all IBIs that had at least 1 fecal sample collected during that phase. Importantly, some of the fecal samples fell during IBIs that did not meet our criteria (see Section 2.3); as a result, only 515 of the total 745 total samples we collected contributed to these analyses (Table 1). We modeled female identity as a random effect (Crawley, 2007). In all models (here and below), variance attributed to random effects was calculated using the *ranova* function in the *lmerTest* package (Kuznetsova et al., 2016). We checked for multicollinearity for model predictors using a form of the variance inflation factor (VIF) analysis adapted for *lmer* models (pers. comm. A. Franks); all VIFs were <2.

**Table 1.** Sample sizes for analyses testing the link between parasite burdens and the duration of IBIs or their component phases.

IBI and its phases	Number of distinct IBIs	Number of female subjects	Number of parasite samples*
PPA	108	76	285
Pregnancy	66	49	123
Cycling	61	52	107
IBI	116	77	392

\*Parasite burdens were averaged across all the samples collected during the IBI or its component phase. Note that 515 total samples contributed to these analyses; this table lists the number of samples that met our criteria for each reproductive state.

### 3.2 The costs of helminths: testing if helminth infection predicts fGCs.

We used a mixed modeling approach to test whether variation in parasite burdens was associated with fGC concentrations. Prior studies in our population find that female fGCs are predicted by rainfall, temperature, reproductive state, and a quadratic effect of group size (Gesquiere et al., 2011, 2008; Markham et al., 2015). Hence, parallel to our models of female IBIs, we first constructed models of fGCs that included reproductive state, rainfall, temperature, group size, and group size squared as fixed effects. As before, we simultaneously added five measures of female parasite risk and used backwards elimination via the step function in *lmerTest* to find the best-fitting model. This best-fitting model always

retained the fixed effects identified as important by prior studies, and it had the potential to include none, one, or more than one of the measures of parasite risk. Because we did not have fGC measures for all fecal samples, the sample size for these analyses was 702 samples from 122 females. Fecal GCs were log transformed in all analyses and fit with a Gaussian error distribution. Following previous analyses of fGCs in our population, individual identity was modeled as a random effects (Gesquiere et al., 2008).

### **3.3 Predictors of parasitism: testing host-, group-, and population-level factors that predict parasitism.**

Finally, we used mixed models to investigate why some females face higher helminth infection risk than others. In these models, our response variables were five measures of helminth infection: (1) log-transformed count of *T. trichiura* eggs; the presence/absence of infection with (2) strongyles, (3) *A. caucasica*, or (4) *S. pigmentatus*; and (5) parasite richness. We used presence/absence for strongyles, *A. caucasica*, *S. pigmentatus* because egg counts within individual samples were low; hence a binomial distribution provided an accurate fit to the data (Table 3). A complete list of the fixed effects we included in our models is summarized in Table 2. To select the best fitting model for each response variable, we again used the step function in the *lmerTest* package (Kuznetsova et al., 2016) to identified the best-supported model using log likelihood ratio tests. Because we were missing data for two of our fixed effects—social connectedness and fGCs—the sample size for these mixed models was 635 samples from 119 females. Log-transformed *T. trichiura* egg counts and parasite richness were modeled using Gaussian error distributions. The presence/absence of infection was modeled using a binomial error structure. Random effects were the identity of the baboon sampled, and the identity of the individual who performed the helminth egg counts.

**Table 2:** Random and fixed effects used in models of parasite risk in baboons.

Predictor	Description
<b>Response variables</b>	
Log <i>T. trichiura</i>	The number of <i>T. trichiura</i> eggs identified in a host sample (1 was added to all counts and then log-transformed)
Strongyles	Presence or absence of strongyles in a given sample
<i>S. pigmentatus</i> infection	Presence or absence of <i>S. pigmentatus</i> in a given sample
<i>A. caucasica</i> infection	Presence or absence of <i>A. caucasica</i> in a given sample
Parasite richness	Count of the distinct parasite taxa identified in a given sample
<b>Random effects</b>	
Individual ID	The identity of the female baboon who contributed the fecal sample.
Observer ID	The identity of the person who identified and counted parasites in the fecal sample.
<b>Fixed effects</b>	
Age	The female's age in years on the day the sample was collected (known to within a few days).
Reproductive state	The female's reproductive state (cycling, lactating, or pregnant) on the day of sample collection.
Fecal glucocorticoids (fGCs)	The concentration of fecal glucocorticoid metabolites (in ng/g) in the fecal sample.
Social status	The ordinal dominance rank of the female in the month of sample collection.
Social connectedness to females	A metric that quantifies the frequency in which each female gave or received grooming to/from adult females, calculated over the year prior to sample collection.
Social connectedness to males	A metric that quantifies the frequency in which each female gave or received grooming to/from adult males, calculated over the year prior to sample collection.
Group size	The total number individuals in the female's social group on the day of sample collection.
Rainfall	The total amount of rainfall (in cm) in the three months prior to sample collection.
Temperature	The average daily maximum temperature in °C in the three months prior to sample collection.
Strongyles	The presence or absence of strongyle eggs in the sample
<i>T. trichiura</i> <sup>A</sup>	The number of <i>T. trichiura</i> eggs counted in the sample. Egg counts were log + 1 transformed prior to analyses.
<i>S. pigmentatus</i> infection <sup>A</sup>	The presence or absence of <i>S. pigmentatus</i> eggs in the sample
<i>A. caucasica</i> infection <sup>A</sup>	The presence or absence of <i>A. caucasica</i> eggs in the sample

<sup>A</sup> Note: presence or intensity of a parasite was not modeled as a predictor variable in cases where the parasite itself was modeled as the response variable.

## 4.0 RESULTS

### 4.1 Helminth prevalence and diversity

Across all 745 samples from 122 females, we identified nine helminth taxa (Table 3). *Trichuris trichiura* was the most common, present in 92.5% of fecal samples and 96.7% of female hosts. Three other helminths were also common: strongyles (61.5% of samples; 89% of females), *A. caucasica* (49.7% of samples; 82% of females), and *S. pigmentatus* (27.7% of samples; 63.1% of females). In addition, we also found five rare parasites: *Strongyloides fulleborni*, *Enterobius vermicularis*, *Acanthocephala* sp., *Primasubulura* sp. and an unknown

trematode. Parasite richness ranged from 0-6 helminth taxa per sample (median= 2 taxa per sample). 97% of samples harbored at least one helminth, and only two out of 122 females did not harbor any helminths.

**Table 3.** Percent of infected hosts and samples, and mean egg counts in infected samples (N = 745 samples from 122 females).

Helminth Taxa	Percent of infected females (n=122)	Percent of infected samples (n=745)	Median egg counts in infected samples
<i>Trichuris trichiura</i>	96.7% (118)	92.5% (689)	53 (range: 1-2759)
Strongyles	89% (103)	61.5% (458)	2 (range: 1-21)
<i>Abbreviata caucasica</i>	82% (100)	49.7% (370)	5 (range: 1-273)
<i>Streptopharagus pigmentatus</i>	63.1% (77)	27.7% (206)	2 (range: 1-25)
<i>Enterobius vermicularis</i>	22.1 % (27)	6.6% (49)	4 (range: 1-1008)
<i>Strongyloides fullerborni</i>	10.7% (13)	1.9% (14)	1 (range: 1-27)
<i>Acanthocephala sp.</i>	4.1% (6)	0.8% (6)	1 (range: 1-20)
<i>Primasubulura sp.</i>	2.7% (4)	0.54% (4)	1 (range: 1-2)
trematode sp.	4.1% (6)	0.8% (6)	1 (range: 1-3)

#### 4.2 Costs of helminth infections: Reproductive and hormonal costs

We found that higher parasite richness, as well as mean egg counts for *T. trichiura*, strongyles, and *S. pigmentatus*, were associated with longer interbirth intervals (IBIs) and/or one of the IBI's component phases (Table 4). IBI durations varied considerably among females; the mean duration was 691 days, ranging from 422 -1223 days. Controlling for other factors known to predict IBIs, higher parasite richness was linked to longer IBIs (Table 4). For every additional parasite species, female IBI duration increased by 45 days (7% of the mean IBI duration). Furthermore, different parasites were associated with each phase of the IBI. Higher *T. trichiura* and *S. pigmentatus* egg counts were associated with longer PPA durations such that a log-fold (base 10) increase in *T. trichiura* egg counts increased PPA duration by approximately 14 days (4% of the observed mean PPA duration) and *S. pigmentatus* by approximately 11 days (3% of the observed mean duration). Higher strongyle egg counts were associated with both longer periods of ovarian cycling before

conception and longer pregnancies (Table 4). Specifically, the addition of 1 strongyle egg increased pregnancy duration by 0.6 days (0.003% of the observed mean gestation).

**Table 4.** Model results for the associations between parasite risk and IBI duration in female baboons (see Table 1 for sample sizes).

IBI component	Fixed effects <sup>1</sup>	Estimate	SE	F	P <sup>2</sup>	Direction of effect
Total IBI duration <sup>3</sup>	rank	5.521	2.201	6.291	0.014	↓low rank ↑ IBI
	primiparity	125.998	31.518	15.98	>0.00	primiparity ↑ IBI
	group size	2.659	2.112	1.586	0.210	NS
	parasite richness	45.075	16.394	7.559	0.007	↑ parasite richness ↑ IBI
PPA duration <sup>4</sup>	rank	3.263	1.694	3.710	0.057	NS
	primiparity	47.918	27.185	3.107	0.081	NS
	group size	0.679	1.624	0.175	0.677	NS
	daily rainfall (mm)	-37.886	28.612	1.753	0.190	NS
	log <i>T. trichiuria</i>	13.739	6.208	4.899	0.029	↑ <i>T. trichiuria</i> ↑ PPA
	<i>S. pigmentatus</i>	11.350	5.356	4.490	0.037	↑ <i>S. pigmentatus</i> ↑ PPA
Cycling duration <sup>5</sup>	Primiparity	54.433	26.426	4.243	0.044	primiparity ↑ cycling
	<i>strongyles</i>	16.616	4.084	16.55	>0.00	↑ <i>strongyles</i> ↑ cycling
Pregnancy duration <sup>6</sup>	daily rainfall	54.433	26.426	0.564	0.456	NS
	<i>strongyles</i>	16.616	4.084	4.830	0.032	↑ <i>strongyles</i> ↑ cycling

<sup>1</sup> Female identity was modeled as a random effect. The standard deviation ( $\sigma$ ), percentages of variance explained (% of  $\sigma^2$ ), and p-values for random effects in each model are given below (from *ranova* in *ImerTest*, Kuznetsova et al., 2016).

<sup>2</sup> Note that some models retain non-significant fixed effects; these variables were significant in Gesquiere et al. (2018)'s more comprehensive analysis, hence we retain them here.

<sup>3</sup> Female identity ( $\sigma = 77.0$ ; % of  $\sigma^2 = 38.5\%$ ; p-value = 0.01); residual ( $\sigma = 97.2$ ; % of  $\sigma^2 = 61.5\%$ )

<sup>4</sup> Female identity ( $\sigma = 62.7$ ; % of  $\sigma^2 = 47.7\%$ ; p-value > 0.001); residual ( $\sigma = 65.6$ ; % of  $\sigma^2 = 52.3\%$ )

<sup>5</sup> Female identity ( $\sigma = 82.2$ ; % of  $\sigma^2 = 78.1\%$ ; p-value = 0.01); residual ( $\sigma = 43.6$ ; % of  $\sigma^2 = 21.9\%$ )

<sup>6</sup> Female identity ( $\sigma = 3.9$ ; % of  $\sigma^2 = 47.8\%$ ; p-value = 0.04); residual ( $\sigma = 4.1$ ; % of  $\sigma^2 = 52.3\%$ )

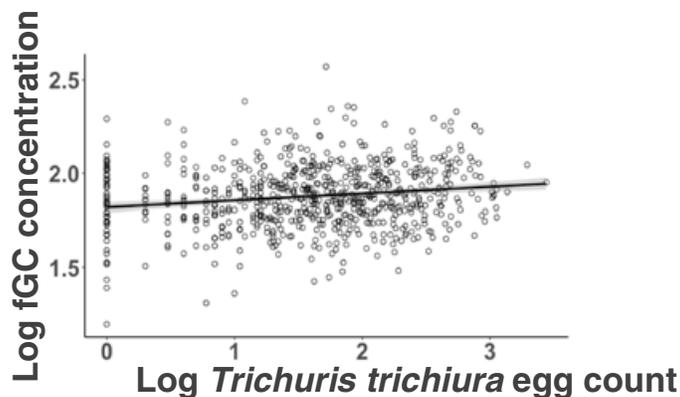
In multivariate analyses, higher *T. trichiura* egg counts were also associated with elevated fGC concentrations (Table 5 and Figure 2). No other measure of parasite burden was significantly associated with host fGC concentrations or improved the model of fGC variation.

**Table 5.** Model results for the associations between parasite risk and fGC concentrations in female baboons (N = 702 samples from 122 females).

Fixed effects <sup>1</sup>	Estimate	SE	F	P <sup>2</sup>	Direction of effect
<i>Log T. trichiura</i>	0.023	0.009	7.115	0.008	↑ <i>T. trichiura</i> ↑GC
rainfall (cm)	-0.006	0.001	36.054	<0.001	↑rainfall ↓GC
temperature	0.028	0.005	29.323	<0.001	↑temperature ↑GC
group size <sup>2</sup>	0.001	0.001	0.022	0.883	NS
group size squared	0.001	<0.001	0.047	0.829	NS
reproductive state (compared to cycling)			10.097		
pregnant	0.061	0.017		<0.001	Pregnancy ↑GC
PPA	-0.002	0.015		0.912	

<sup>1</sup> Female identity was modeled as a random effect. Female identity ( $\sigma = 0.04$ , % of  $\sigma^2 = 21.4\%$  and p-value <0.01; residual ( $\sigma = 0.15$ , % of  $\sigma^2 = 78.6\%$ ).

<sup>2</sup> Note that some models retain non-significant fixed effects (notably group size and its square); these variables were significant in more comprehensive analyses (Gesquiere et al., 2008; Markham et al., 2015), hence we retain them here.



**Fig. 2.** Plot showing the relationship between log-transformed *Trichuris trichiura* egg counts and log-transformed fecal glucocorticoid concentrations.

#### 4.3 Multi-scale predictors of female parasitism

*Host-level predictors.* At the level of individual hosts, old age, co-infection, and social connectedness were all associated with helminth burdens (Table 6). Specifically, older females exhibited higher *T. trichiura* egg counts than younger females (Fig.3A). With respect to co-infection, *T. trichiura* and strongyles were positively associated such that samples from females infected with strongyles typically harbored 21 more *T. trichiura* eggs than samples from females not infected by strongyles (Fig. 3B). In addition, infection by *S. pigmentatus*

was associated with the risk of *A. caucasica* infection (Table 6); the likelihood of infection by *A. caucasica* was 16% higher in individuals infected by *S. pigmentatus* compared to uninfected females.

The relationships between social connectedness and parasitism were complex. For *T. trichiura*, females who were socially isolated from adult males harbored higher egg counts than females socially connected to adult males (Table 6, Fig. 3C). For parasite richness, females who were socially isolated from adult females were infected with more helminth taxa than females were socially connected to other females. Females with high social connectedness to adult males had a higher probability of *A. caucasica* infection than females with low social connectedness to males (Table 6). Finally, the random effect estimates indicated that fairly substantial fractions of variance were attributed to unaccounted for aspects of host identity (% of residual variance ranged from 24% to 75%; Table 6).

*Group-level predictors.* At the group level, females living in large groups exhibited high *T. trichiuris* egg counts, but were less likely to be infected by strongyles (Fig.3D, Table 6). The risk of strongyle infection risk was 9.5% lower for females living in the largest third of group sizes (74 to 118 individuals) compared to females living in the smallest third of group sizes (21 to 48 individuals). However, this effect was only significant when *T. trichiura* was included in the model, suggesting that these effects are amplified by the positive covariation between *T. trichiura* and strongyles. Females in larger groups were also more likely to be infected by *A. caucasica* than females in smaller groups (Table 6).

*Population-level predictors.* At the population level, low rainfall and low temperatures tended to be associated with higher helminth infection risk (Table 6). Females exhibited the highest *T. trichiura* egg counts during cool, dry periods (Fig. 3E and 3F). Females living in low rainfall environments also had higher risk of *A. caucasica* infection, but were less likely to be infected by *S. pigmentatus*. Notably, samples collected in low rainfall periods were 24% less likely to contain *A. caucasica* eggs while samples collected during high rainfall periods were 8% more likely to contain *S. pigmentatus* eggs.

**Table 6.** Best supported models of predictors of parasite risk in female baboons based on likelihood ratio tests (N = 635 samples from 119 females).

Helminth taxa	Fixed effects <sup>1</sup>	Process level	Estimate	SE	F	P	Direction of effect
Log <i>T. trichiura</i> <sup>3</sup>	age	Individual	0.031	0.009	12.483	0.001	↑ age ↑ <i>T. trichiura</i>
	<i>strongyles</i>	Individual	0.237	0.053	19.874	0.000	↑ <i>strongyles</i> ↑ <i>T. trichiura</i>
	SCI <sup>2</sup> to males	Individual	-0.057	0.025	5.254	0.022	↑ connectedness ↓ <i>T. trichiura</i>
	group size	Group	0.009	0.001	35.086	0.000	↑ group size ↑ <i>T. trichiura</i>
	rainfall	Population	-0.022	0.004	25.185	0.000	↑ rainfall ↓ <i>T. trichiura</i>
	temperature	Population	-0.062	0.023	7.414	0.007	↑ temperature ↓ <i>T. trichiura</i>
<i>Strongyles</i> <sup>4</sup>	<i>T. trichiura</i>	Individual	0.746	0.142	25.223	0.000	↑ <i>T. trichiura</i> ↑ <i>strongyles</i>
	group size	Group	-0.012	0.005	5.564	0.023	↑ group size ↓ <i>strongyles</i>
<i>A. caucasica</i> <sup>5</sup>	<i>S. pigmentatus</i>	Individual	0.669	0.223	3.628	0.002	↑ <i>S. pigmentatus</i> ↑ <i>A. caucasica</i>
	SCI <sup>2</sup> to males	Individual	0.251	0.092	6.000	0.006	↑ connectedness ↑ <i>A. caucasica</i>
	group size	Group	0.013	0.005	2.513	0.011	↑ group size ↑ <i>A. caucasica</i>
	rainfall	Population	-0.083	0.014	40.105	0.000	↑ rainfall ↓ <i>A. caucasica</i>
<i>S. pigmentatus</i> <sup>6</sup>	<i>A. caucasica</i>	Individual	0.597	0.216	4.574	0.006	↑ <i>A. caucasica</i> ↑ <i>S. pigmentatus</i>
	rainfall	Population	0.038	0.014	8.009	0.007	↑ rainfall ↑ <i>S. pigmentatus</i>
Parasite richness	SCI <sup>2</sup> to females	Individual	-0.147	0.055	7.183	0.008	↑ connectedness ↓ richness
	temperature	Population	-0.092	0.026	12.143	0.001	↑ temperature ↓ richness

<sup>1</sup> Random effects were female identity and identity of person who counted the parasites (observer). The standard deviation ( $\sigma$ ), percentages of variance explained (% of  $\sigma^2$ ), and p-values for random effects in each model are given below (from ranova in *ImerTest*, Kuznetsova et al., 2016).

<sup>2</sup> Social connectedness index

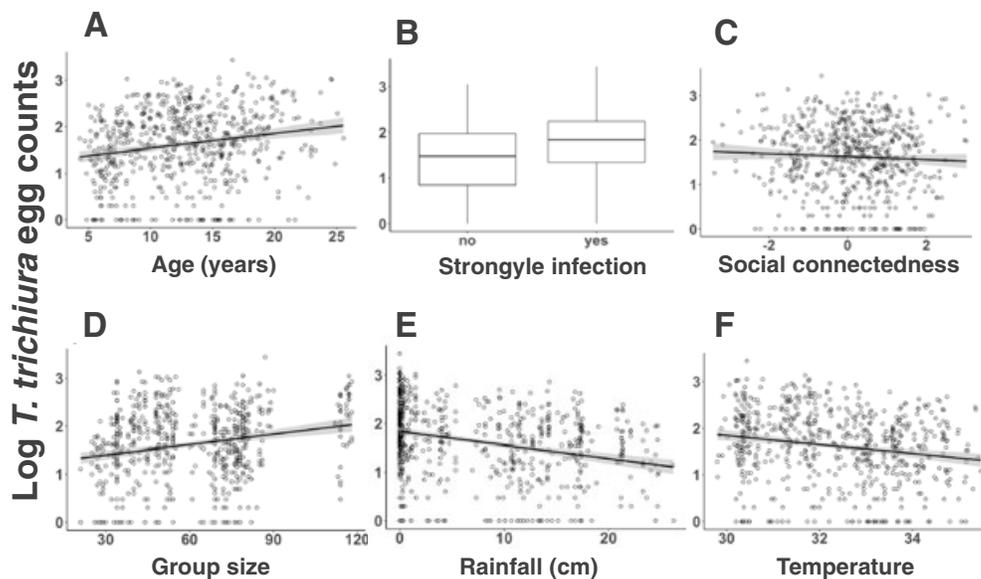
<sup>3</sup> Female identity ( $\sigma = 0.35$ ; % of  $\sigma^2 = 26.8\%$ ; p-value <0.001); observer ( $\sigma = 0.13$ ; % of  $\sigma^2 = 3.6\%$ ; p-value <0.001); residual ( $\sigma = 0.57$ ; % of  $\sigma^2 = 69.6\%$ ).

<sup>4</sup> Female identity ( $\sigma = 0.95$ ; % of  $\sigma^2 = 21.0\%$ ; p-value <0.001); observer ( $\sigma = 0.31$ ; % of  $\sigma^2 = 2.2\%$ ; p-value = 0.19); residual ( $\sigma = 1.81$ ; % of  $\sigma^2 = 76.8\%$ ).

<sup>5</sup> Female identity ( $\sigma = 0.83$ , % of  $\sigma^2 = 16.4\%$ ; p-value <0.001); observer ( $\sigma = 0.42$ ; % of  $\sigma^2 = 4.3\%$ ; p-value <0.001); residual ( $\sigma = 1.83$  (% of  $\sigma^2 = 79.3\%$ )).

<sup>6</sup> Female identity ( $\sigma = 0.72$ ; % of  $\sigma^2 = 11.5\%$ ; p-value <0.001); observer ( $\sigma = 0.83$ ; % of  $\sigma^2 = 15.3\%$ ; p-value <0.001); residual ( $\sigma = 1.81$ ; % of  $\sigma^2 = 73.2\%$ ).

<sup>7</sup> Female identity ( $\sigma = 0.39$ , % of  $\sigma^2 = 14.7\%$ ; p-value <0.001); observer ( $\sigma = 0.28$ ; % of  $\sigma^2 = 7.9\%$ ; p-value <0.001); residual ( $\sigma = 0.89$ ; % of  $\sigma^2 = 77.4\%$ ).



**Figure 3.** Association between log *T. trichiura* egg counts and (A) presence/absence of strongyle infection; (B) female social connectedness to adult males; (C) age in years; (D) group size; (E) rainfall in the previous 3 months (cm); (F) average maximum temperature in the previous 3 months.

## 5.0 DISCUSSION

Understanding the costs and drivers of parasitism in wild mammals is important, both for learning which selection pressures shape behavior and life histories, and for managing and conserving natural populations. Our study adds to mounting evidence that helminths impose costs on wild female primates (Nguyen et al., 2015). Specifically, we found that elevated parasite richness is associated with low female fertility. As such, coinfection by a diverse community of helminths may contribute to variation reproductive success in female baboons and have repercussions for baboon population dynamics. Moreover, by testing more factors than any other study to date (Tables S1 and S2), we contribute an unusually holistic understanding of the causes and consequences of helminth infection. Our analyses indicate that processes operating at several levels—individual hosts, social groups, and the population at large—all predict variation in female parasite risk. Across parasites, female infection risk was most often associated with old age, social isolation, living in dry conditions, and infection with other helminth species. All of these factors may predict parasite exposure or susceptibility, and further research will be needed to understand the mechanisms underlying these patterns.

With respect to the costs of parasitism, we found a correlation between helminth burdens and female interbirth intervals. Specifically, parasite richness, *T. trichiura* and/or strongyle egg counts were associated, either with long IBIs, or with long durations for one of the IBIs components (e.g. PPA, cycling, pregnancy). These findings were consistent with a previous study in primates by Nguyen et al., (2015), which found that female gelada baboons infected by *Taenia* species (tapeworms) exhibit longer IBIs. Similarly, experimental research in other mammals has shown that experimentally reducing endo- and ecto-

parasites sometimes increases female reproductive success (Hillegass et al., 2010; Neuhaus, 2003; Patterson and Ruckstuhl, 2013) but see (Raveh et al., 2015). The mechanisms by which parasites prolong IBIs are difficult to assess in natural populations. One possibility is that helminth infections damage host tissues and/or lead to costly immune responses, which in turn deplete host energetic resources required to support reproduction. This mechanism is consistent with recent research on the Amboseli baboons, which finds that female IBIs are longer under energetically stressful conditions, including when females are living in large social groups, in quality habitats, and have low social dominance rank (Gesquiere et al., 2018).

Another possible mechanism is that helminth infections elicit immune responses that in turn interfere with host reproduction via neuroimmunoendocrine responses (Nava-Castro et al., 2011). This mechanism may partly explain why we observed different relationships between the different parasites and each of the IBI's component phases. Specifically, while parasite richness was linked to longer overall interbirth intervals, *T. trichiura* was more tightly linked to PPA duration, while strongyle infection was linked to longer periods of ovarian cycling and longer gestations. We speculate that these differences could be driven by possible interactions between parasites, immune system, and the endocrine system during each of these reproductive phases. Host hormones released during each phase may influence host immune responses or may directly affect parasite growth, differentiation, or reproduction (Escobedo et al., 2005; Hernández-Bello et al., 2010; Klein, 2000; Romano et al., 2015). In turn, these effects may increase or reduce parasite susceptibility and resistance. Moreover, different parasites elicit different immune response or respond differently to circulating host hormones (Klein, 2000), which may also contribute to differential relationships between parasite species and female reproductive phases. Further research is necessary to understand how different parasite species both influence and are influenced by female reproductive physiology. Finally, we acknowledge the possibility that greater parasite richness might occur as a consequence of longer IBIs if richness is highly dependent upon a strongly cumulative process. However, we also note that this explanation

is unlikely because we see no significant effect of host age, implying that parasite richness is not a strongly cumulative process in our population.

In addition to reproductive costs, we also found that higher *T. trichiura* egg counts were associated with elevated fGC concentrations. The relationship between parasitism and host glucocorticoids is often complex in natural populations, but a handful of other studies in primates have also reported positive associations between host glucocorticoids and helminth burdens (Arlet et al., 2015; Muehlenbein and Watts, 2010; Müller-Klein et al., 2018). Furthermore, a recent experimental study on free ranging mangabeys found that parasite removal led to a reduction in host GC levels (Friant et al., 2016). Several processes may contribute to the positive relationships we observed between *T. trichiuris* and fGC in female baboons. First, this relationship may reflect the energetic costs of either coping with tissue damage caused by *T. trichiuris* or resisting *T. trichiuris* infection. In support, prior research in Amboseli finds that fGC concentrations are highest in female baboons during energetically costly periods, including during the dry season, hot weather, pregnancy, and when females live in extremely large or small groups (Gesquiere et al., 2008; Markham et al., 2015). Second, fGCs are known to have anti-inflammatory and immunosuppressive effects; hence individuals with chronically elevated GCs may be less able to resist *T. trichiuris* infections. We did not find evidence that high quality females are able to sustain high GCs, high reproductive effort, and resist parasites, at least in the subjects and study years included here.

With respect to multi-scale drivers of helminth infection, we found several patterns that were common across the different helminth taxa. At the level of individual hosts, the dominant drivers of female parasite risk were social connectedness, age, reproductive state, and coinfection. In particular, we found positive associations between three pairs of parasites 1) *T. trichiura* and strongyles, 2) *A. caucasica* and *S. pigmentatus* and 3) *T. trichiura* and *S. pigmentatus*. At least three, non-mutually exclusive mechanisms may contribute to these patterns. First, shared transmission modes among helminth parasites may increase the likelihood that different heminth species co-occur in the same host

(Fleming et al., 2006). In support, in our data, the species transmitted via fecal-oral routes, *T. trichiura* and strongyles, tended to co-occur. Likewise, both helminths transmitted by insect intermediate hosts, *A. caucasica* and *S. pigmentatus*, were also likely to infect the same hosts. Second, helminth associations may be immune-mediated such that infection by one species dampens immune responses to additional infections (Pedersen and Fenton, 2007). Third, there may be a vicious cycle between parasite infection and body condition, such that infection by one parasite leads to poor body condition, which has consequences for a host's ability to resist subsequent infections. Hence, hosts will be unable to fight off additional infections by more parasites. Interestingly, we found no evidence that parasites compete for infection sites or host tissues in our population, suggesting that this mechanism does not contribute substantially to patterns of parasite risk for these specific parasite taxa in our population.

We also found that social isolation was associated with higher *T. trichiura* egg counts and parasite richness. This finding supports research linking social isolation with morbidity and mortality (Archie et al., 2014; Holt-Lunstad et al., 2010; Uchino, 2006). However, it contradicts the idea that social connectedness leads to elevated parasite exposure and helminth burdens (MacIntosh et al., 2012; Rimbach et al., 2015). Contrary to our findings in females, a parallel study on male baboons in Amboseli by Habig et al. (in review) found that male social connectedness to female baboons was linked to higher *T. trichiura* egg counts and higher parasite richness in, suggesting either that host contact (increased exposure) leads to parasite transmission in males, or males investing in female mating effort experience tradeoffs with immune function that increase parasite susceptibility. In females, we also found one helminth that exhibited a positive association with social connectedness, *A. caucasica*, which is transmitted via an insect vector. For this parasite, it may be that social connectedness is associated with access to the best food resources, including insects, which may be high in fat and protein.

Consistent with prior research on primates (Table S1), for both parasite richness and *T. trichuris*, we found 'type I' age-intensity curves, which show a positive correlation between age and helminth burden (Wilson et al., 2002). This profile can be attributed to both increased exposure to parasites over an individual's life and host immuno-senescence (Nunn and Altizer, 2006; Wilson et al., 2002). Disentangling the effects of exposure and immuno-senescence on worm burden is challenging in wild populations. Adult *T. trichiura* are thought to live for 1 to 2 years (Cogswell, 2007; Anderson, 2000). Equally strikingly, some strongyles may live for 8-15 years (Table S1, Habig et al. in review). The relatively long lives of these helminths would contribute to a pattern in which hosts accumulate these parasites as they age, leading to higher egg shedding at older ages.

Under group level processes, group size predicted female parasite risk, though in conflicting ways. Prior meta-analyses in vertebrates have found that infection risk frequently increases with group size (Cote and Poulin, 1995; Patterson and Ruckstuhl, 2013; Rifkin et al., 2012). We found mixed support for this pattern: females in larger groups exhibited higher *T. trichiuris* egg counts, but lower strongyle infection risk. Parasite-specific differences in exposure might explain these inconsistent relationships with group size. For instance, *T. trichiura* is transmitted through fecal contamination in the environment; hence members of larger groups may live at higher social densities and encounter fecal contamination from group members more frequently than baboons living in smaller groups. While strongyles are also transmitted via fecal-oral routes, this taxonomic grouping likely includes multiple parasite species, and some may be generalist parasites that infect co-resident ungulates as well as baboons (Archie and Ezenwa, 2011). If true, the density of baboon hosts in an individual's social group may be less important in predicting individual infection risk than the density of other host species. In terms of susceptibility-mediated processes, female baboons in larger groups in Amboseli may experience more intense competition for resources than those in smaller groups and hence may be less able to mount effective immune responses to infection.

With respect to population-level processes, low rainfall and low temperatures were both associated with elevated helminth risk. Contrary to most prior studies, baboons in Amboseli exhibited higher *T. trichiura* egg counts and greater *A. caucasica* and *S. pigmentatus* risk in dry as compared to rainy periods. In most helminths, rain and high humidity enhance the survival of parasite infectious stages; hence parasite exposure should be highest during wet periods (Altizer et al., 2006). However, rainfall directly affects food availability, which in turn affects host nutrition and the host's ability to mount effective immune responses against helminths (Dowell, 2001; Hawley and Altizer, 2011; Koski and Scott, 2001; Martin et al., 2008). During the dry season, baboons in Amboseli feed on foods that require extensive processing for relatively small nutritional rewards, such as grass corms, whereas in the wet season they feed on more diverse and easily harvested foods (Alberts et al., 2005; Altmann, 1998). In addition, during dry periods, baboons spend more time foraging and searching for food and water thus increasing their energetic expenditure relative to periods with adequate rainfall (Alberts et al., 2005; Gesquiere et al., 2008). Thus, the dry season in Amboseli is associated with greater nutritional stress, probably resulting in poorer health, which in turn could contribute to higher helminth burdens (Crompton and Nesheim, 2002). In addition, negative correlations between rainfall and helminth burden could be explained by the "wash away effect", whereby heavy rainfall washes away parasite infectious stages and decreases host exposure (Meade, 1983; Poirotte et al., 2016).

In conclusion, our study adds to the limited data on the costs that helminth infections impose on wild populations. By testing multi-scale processes, we provide an especially holistic understanding of processes influencing infection risk in a wild population. Because of the challenges of longitudinal monitoring in wild populations, our study relied heavily on opportunistic sampling. Future studies can aim at having systematic sample collection to maximize on sample sizes and to control for the probability of intermittent shedding of fecal eggs.

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## AUTHORS' CONTRIBUTIONS

MA, DJ, SCA, BH, and EAA designed the study; MA, BH, LG, SCA, and EAA collected data; MA and DJ analyzed the data; MA, SCA, and EAA wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Data available from the Dryad Data Repository: <http://doi.org/10.5061/dryad.m80f888> (Akinyi et al. 2019).

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