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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 (a) examine the costs of helminth infections in terms of female fertility and glucocorticoid hormone levels and (b) 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 faecal samples collected over 5 years from 122 female baboons. We combine these data with detailed observations of host environments, social behaviours, hormone levels and interbirth intervals (IBIs).
4. We found that helminths are costly to female fertility: females infected with more diverse parasite communities (i.e., higher parasite richness) exhibited longer IBIs 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.

KEYWORDS
baboons, female fertility, fitness costs, glucocorticoid hormones, helminth infection, primates, *Trichuris trichiura*

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*These authors contributed equally to this manuscript.

1 | INTRODUCTION

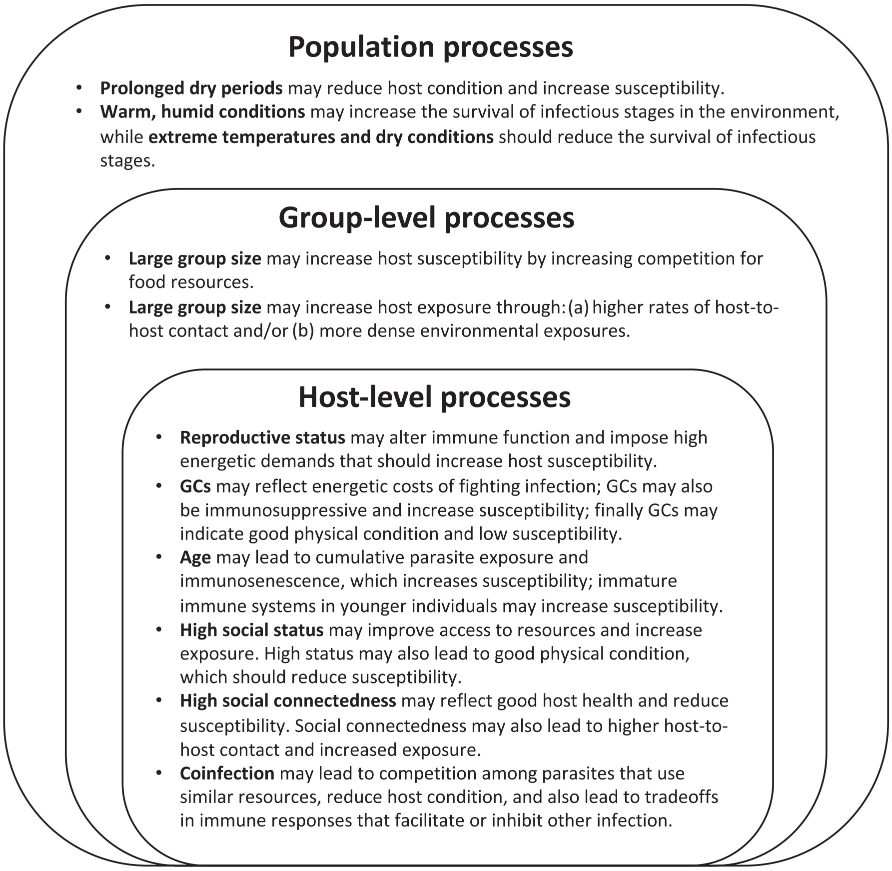
In humans and domestic animals, the costs of helminth parasitism are well known, with wide-ranging effects on host growth, reproduction, mortality and susceptibility to other parasites (Bethony et al., 2006; Charlier, Voort, Kenyon, Skuce, & Vercruysse, 2014; Hotez et al., 2008). However, studies that 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 behaviour and life histories, identify individuals that are most at risk and inform management strategies in vulnerable populations (Kaur & Singh, 2009; Tompkins & 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 & 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 & Nesheim, 2002; Koski & 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, Krasnov, Kam, Burdelova, & Degen, 2002; McFalls, Joseph, & McFalls, 1984). In support, the experimental removal of ecto- and endoparasites sometimes leads to increased reproductive success (Hillegass, Waterman, & Roth, 2010; Neuhaus, 2003; Patterson & Ruckstuhl, 2013, but see Gooderham & Schulte-Hostedde, 2011; Raveh, Neuhaus, & Dobson, 2015; Raveh et al., 2011). In primates, previous research by Nguyen et al. (2015) found that female gelada baboons infected by *Taenia* species exhibit longer interbirth intervals (IBIs) (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 first birth and short IBIs, whereas infection with hookworm is associated with late age at first pregnancy and long IBIs.

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, Ziegler, & Goldberg, 2016; Muehlenbein & Watts, 2010; Müller-Klein et al., 2018; Sures, Knopf, & Kloas, 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, Millspaugh, Washburn, Brundige, & Raedeke, 2005; Monello, Millspaugh, Woods, & Gompper, 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 & 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, which regulates the T-helper 2 system important for clearing helminth infections (Helmby & 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 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 behavioural strategies and social structures, and point to selection pressures and constraints that have shaped mammalian behaviour 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 Figure 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: (a) host exposure to helminth infectious stages and (b) 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, Nakagawa, Rhodes, & Simmons, 2017; Nunn & Altizer, 2006; Rushmore, Bisanzio, & Gillespie, 2017; Vitone, Altizer, & Nunn, 2004; Wilson et al., 2002; Zuk & 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



Population processes

- **Prolonged dry periods** may reduce host condition and increase susceptibility.
- **Warm, humid conditions** may increase the survival of infectious stages in the environment, while **extreme temperatures and dry conditions** should reduce the survival of infectious stages.

Group-level processes

- **Large group size** may increase host susceptibility by increasing competition for food resources.
- **Large group size** may increase host exposure through: (a) higher rates of host-to-host contact and/or (b) more dense environmental exposures.

Host-level processes

- **Reproductive status** may alter immune function and impose high energetic demands that should increase host susceptibility.
- **GCs** may reflect energetic costs of fighting infection; GCs may also be immunosuppressive and increase susceptibility; finally GCs may indicate good physical condition and low susceptibility.
- **Age** may lead to cumulative parasite exposure and immunosenescence, which increases susceptibility; immature immune systems in younger individuals may increase susceptibility.
- **High social status** may improve access to resources and increase exposure. High status may also lead to good physical condition, which should reduce susceptibility.
- **High social connectedness** may reflect good host health and reduce susceptibility. Social connectedness may also lead to higher host-to-host contact and increased exposure.
- **Coinfection** may lead to competition among parasites that use similar resources, reduce host condition, and also lead to tradeoffs in immune responses that facilitate or inhibit other infection.

FIGURE 1 Processes proposed to drive inter-host variation in helminth infection risk in female savanna 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

competition and high parasite exposure, which can lead to high helminth burdens (Cote & Poulin, 1995; Kappeler, Cremer, & Nunn, 2015; Rifkin, Nunn, & Garamszegi, 2012). Population processes such as rainfall and temperature may determine the survival of parasite infectious stages in the environment, host physical condition and host behaviour, all of which have consequences for parasite exposure and susceptibility (Nunn & 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, Ezenwa, Etienne, Turner, & Olff, 2008; Pedersen & 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 amenorrhoea (PPA) (Beehner, Nguyen, Wango, Alberts, & Altmann, 2006; Gesquiere, Wango, Alberts, & Altmann, 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 matrilocal, 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 (a) identify the costs of helminth infection on female baboons, as evidenced by links to measures of female fertility and GC hormones, and (b) test how host-, group- and population-level processes predict female infection risk. For the first objective, we used female 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 component phases: 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, Altmann, Archie, & Alberts, 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 GCs, 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.

2 | MATERIALS AND METHODS

2.1 | Study population and site

The Amboseli ecosystem in Kenya (2°40′S, 37°15′E, 1,100 m) is a semi-arid short-grass savanna that is home to a population of wild baboons monitored by the Amboseli Baboon Research Project (ABRP) (Alberts & Altmann, 2012; Alberts et al., 2005). Observers collect behavioural, environmental and demographic data on the members of 4–6 study groups at any given time; each study group is monitored 2–4 days each week (Alberts & 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 | Faecal sample collection and parasitology

Faecal 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 nine 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 datasets were collected, including the duration of IBIs in Section 2.32.3; we discuss faecal GC concentrations in Section 2.42.4, and other host, group and population drivers of parasitism in Section 2.52.5. We then describe how sample-specific parasite data were used as predictors of female fertility in Section 2.6.1 and as predictors of faecal GC concentrations in Section 2.6.2. Finally, in Section 2.6.3, we describe our modelling 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 IBIs as a measure of female fertility. To measure IBIs and their component phases—PPA, sexual cycling and pregnancy—ABRP collects continuous, individual-based data on female sexual swellings, colour changes to the paracallosal skin and menstrual bleeding, allowing us to track female reproductive state with high accuracy (Beehner et al., 2006; Fitzpatrick, Altmann, & Alberts, 2014; Gesquiere et al., 2007). We measured IBI durations using the same methods as Gesquiere et al. (2018), which conducted a comprehensive analysis of IBIs 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 faecal glucocorticoid concentrations

To test whether parasites impose costs that are reflected in female GC levels, we measured faecal glucocorticoid (fGC) concentrations in 702 of the 745 faecal samples where we had also measured parasitism (mean = 5.75 samples per individual; range = 1–24 samples). Briefly, faecal 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 faecal powder (0.2 g) underwent extraction in 90% methanol, followed by solid phase extraction using Waters Oasis HLB cartridges. Faecal GC (fGC) metabolites in the samples were measured in ng per g of dried faeces by radioimmunoassays, following a well-established protocol (e.g., Gesquiere, Onyango, Alberts, & Altmann, 2011; Gesquiere et al., 2008; Markham, Gesquiere, Alberts, & Altmann, 2015; Onyango, Gesquiere, Wango, Alberts, & Altmann, 2008). We used the Corticosterone kit for Rats and Mice (ICN diagnostics) which has previously been validated for our population (Gesquiere et al., 2005;

Khan, Altmann, Isani, & Yu, 2002; Lynch, Khan, Altmann, Njahira, & Rubenstein, 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.

2.5.1 | Host-level predictors

Age on the day of faecal sample collection was known within a few days and modelled 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 4.25–25.45 years (mean = 12.61 years).

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

Faecal 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, Romero, & Munck, 2000). Hence, in addition to testing whether parasite burdens predicted GCs, we also included fGC concentrations (measured in the same faecal 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, Silk, & Altmann, 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, Tung, Clark, Altmann, & Alberts, 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.

2.5.2 | 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 modelled as a continuous variable and is known from near-daily censuses of all the members of each social group.

2.5.3 | Population-level predictors

Amboseli experiences a dry season between June and October, and a wet season between November and May (Gesquiere et al., 2011). Rainfall is highly variable, ranging from 150 to 750 mm/year, with a mean of 344 mm/year (Alberts et al., 2005; Altmann, Alberts, Altmann, & Roy, 2002). Temperatures ranged between 28 and 35°C (mean = 32.30°C). We modelled climate variables using *total rainfall* and *average maximum daily temperature* in the 3 months prior to sample collection. We chose a 3-month period for two reasons: (a) 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 (b) 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.

2.6 | Statistical analyses

2.6.1 | The costs of helminths: testing if helminth infection is linked to longer IBIs

We used a mixed modelling 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, Machler, Bolker, & Walker, 2015) and *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2016). We built separate models for each of the four response variables, which were durations in days for (a) the full IBI (*N* = 116 IBIs from 77 females), (b) PPA (*N* = 108 PPAs from 76 females), (c) ovarian cycling (*N* = 61 periods of ovarian cycling from 52 females) and (d) 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 re-creating 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 dataset 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 faecal samples collected during each IBI or component phase for (a) *T. trichiura* (because these counts were not normal, 1 was added to all counts and log-transformed), (b) strongyles, (c) *A. caucasica*, (d) *S. pigmentatus* and (e) mean parasite richness as a count of the number of different helminth taxa observed in each faecal sample. Our sample sizes for these analyses (Table 1) included all IBIs that had at least one faecal sample collected during that phase. Importantly, some of the faecal samples fell during IBIs that did not meet our criteria (see Section 2.32.3); as a result, only 515 of the total 745 total samples we collected contributed to these analyses (Table 1). We modelled 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 (A. Franks, pers. comm.); all VIFs were <2.

2.6.2 | The costs of helminths: testing if helminth infection predicts fGCs

We used a mixed modelling 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., 2008, 2011; 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 faecal samples, the sample size for these analyses was 702 samples from 122 females. Faecal 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 modelled as a random effects (Gesquiere et al., 2008).

2.6.3 | 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: (a) log-transformed count of *T. trichiura* eggs; the presence/absence of infection with (b) strongyles, (c) *A. caucasica* or (d) *S. pigmentatus*; and (e) parasite richness. We used presence/absence for strongyles, *A. caucasica* and *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 modelled using Gaussian error distributions. The presence/absence of infection was modelled 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.

3 | RESULTS

3.1 | 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 faecal 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 to 6 helminth taxa per sample (median = 2 taxa per sample). 97% of samples harboured at least one helminth, and only two out of 122 females did not harbour any helminths.

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[a]
PPA	108	76	285
Pregnancy	66	49	123
Cycling	61	52	107
IBI	116	77	392

Note.: Abbreviation: IBI, interbirth intervals.

[a] 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.

TABLE 2 Random and fixed effects used in models of parasite risk in baboons

Predictor	Description
Response variables	
Log *Trichuris trichiura*	The number of *T. trichiura* 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
Streptopharagus pigmentatus infection	Presence or absence of *S. pigmentatus* in a given sample
Abbreviata caucasica infection	Presence or absence of *A. caucasica* in a given sample
Parasite richness	Count of the distinct parasite taxa identified in a given sample
Random effects	
Individual ID	The identity of the female baboon who contributed to the faecal sample
Observer ID	The identity of the person who identified and counted parasites in the faecal sample
Fixed effects	
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
Faecal glucocorticoids (fGCs)	The concentration of faecal glucocorticoid metabolites (in ng/g) in the faecal 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 females, calculated over the year prior to sample collection
Group size	The total number of individuals in the female's social group on the day of sample collection
Rainfall	The total amount of rainfall (in cm) in the 3 months prior to sample collection
Temperature	The average daily maximum temperature in °C in the 3 months prior to sample collection
Strongyles	The presence or absence of strongyle eggs in the sample
T. trichiura[a]	The number of *T. trichiura* eggs counted in the sample. Egg counts were log + 1-transformed prior to analyses
S. pigmentatus infection[a]	The presence or absence of *S. pigmentatus* eggs in the sample
A. caucasica infection[a]	The presence or absence of *A. caucasica* eggs in the sample

[a] Presence or intensity of a parasite was not modelled as a predictor variable in cases where the parasite itself was modelled as the response variable.

3.2 | 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*, was associated with longer 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 to 1,223 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 one strongyle egg increased pregnancy duration by 0.6 days (0.003% of the observed mean gestation).

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.

3.3 | Multi-scale predictors of female parasitism

3.3.1 | 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 (Figure 3a). With respect to co-infection, *T. trichiura* and strongyles were positively associated such that samples from females infected with strongyles typically harboured 21 more *T. trichiura* eggs than samples from females not infected by strongyles (Figure 3b). In addition, infection by *S. pigmentatus* was associated with the risk of

TABLE 3 Per cent of infected hosts and samples, and mean egg counts in infected samples ($N = 745$ samples from 122 females)

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

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[a]	Estimate	*SE*	*F*	*p*[b]	Direction of effect
Total IBI duration[c]	Rank	5.521	2.201	6.291	0.014	↓Low rank ↑ IBI
	Primiparity	125.998	31.518	15.981	>0.001	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[d]	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 *T. trichiuria*	13.739	6.208	4.899	0.029	↑ *T. trichiuria* ↑ PPA
	S. pigmentatus	11.350	5.356	4.490	0.037	↑ *S. pigmentatus* ↑ PPA
Cycling duration[e]	Primiparity	54.433	26.426	4.243	0.044	primiparity ↑ cycling
	Strongyles	16.616	4.084	16.553	>0.001	↑ *Strongyles* ↑ cycling
Pregnancy duration[f]	Daily rainfall	54.433	26.426	0.564	0.456	NS
	Strongyles	16.616	4.084	4.830	0.032	↑ *Strongyles* ↑ pregnancy

Note.: Abbreviation: PPA, pregnancy and postpartum amenorrhoea.

[a] Female identity was modelled as a random effect. The standard deviation (σ), percentages of variance explained (% of σ^2) and p-values for random effects in each model are given below (from ranova in *lmerTest*, Kuznetsova et al., 2016).

[b] 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.

[c] Female identity ($\sigma = 77.0$; % of $\sigma^2 = 38.5\%$; p-value = 0.01); residual ($\sigma = 97.2$; % of $\sigma^2 = 61.5\%$).

[d] Female identity ($\sigma = 62.7$; % of $\sigma^2 = 47.7\%$; p-value > 0.001); residual ($\sigma = 65.6$; % of $\sigma^2 = 52.3\%$).

[e] Female identity ($\sigma = 82.2$; % of $\sigma^2 = 78.1\%$; p-value = 0.01); residual ($\sigma = 43.6$; % of $\sigma^2 = 21.9\%$).

[f] Female identity ($\sigma = 3.9$; % of $\sigma^2 = 47.8\%$; p-value = 0.04); residual ($\sigma = 4.1$; % of $\sigma^2 = 52.3\%$).

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 harboured higher egg counts than females socially connected to adult males (Table 6, Figure 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).

3.3.2 | 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 (Figure 3d, Table 6). The risk of strongyle infection risk was 9.5%

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

Fixed effects[a]	Estimate	*SE*	*F*	p^2	Direction of effect
Log *T. trichiura*	0.023	0.009	7.115	0.008	↑*T. trichiura* ↑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[b]	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	

Note.: Abbreviation: PPA, pregnancy and postpartum amenorrhoea.

[a] Female identity was modelled as a random effect. Female identity (σ = 0.04, % of σ^2 = 21.4% and p-value <0.01; residual (σ = 0.15, % of σ^2 = 78.6%).

[b] 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.

lower for females living in the largest third of group sizes (74–118 individuals) compared to females living in the smallest third of group sizes (21–48 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).

3.3.3 | 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 (Figure 3e,f). 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.

4 | DISCUSSION

Understanding the costs and drivers of parasitism in wild mammals is important, both for learning which selection pressures shape behaviour 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, co-infection 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.

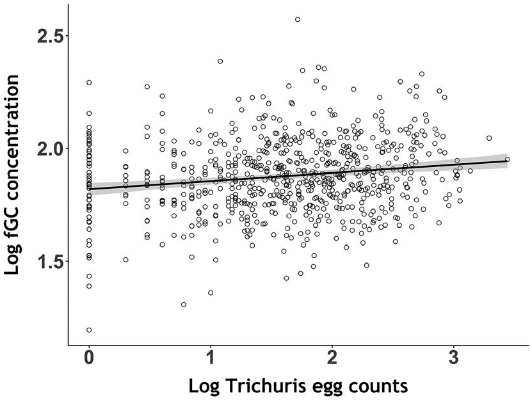


FIGURE 2 Plot showing the relationship between log-transformed *Trichuris trichiura* egg counts and log-transformed faecal glucocorticoid concentrations

With respect to the costs of parasitism, we found a correlation between helminth burdens and female IBIs. Specifically, parasite richness, *T. trichiuira* 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

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[a]	Process level	Estimate	*SE*	*F*	*p*	Direction of effect
Log *T. trichiura*[b]	Age	Individual	0.031	0.009	12.483	0.001	↑ age ↑ *T. trichiura*
	Strongyles	Individual	0.237	0.053	19.874	0.000	↑ strongyles ↑ *T. trichiura*
	SCI to males	Individual	−0.057	0.025	5.254	0.022	↑ connectedness ↓ *T. trichiura*
	Group size	Group	0.009	0.001	35.086	0.000	↑ group size ↑ *T. trichiura*
	Rainfall	Population	−0.022	0.004	25.185	0.000	↑ rainfall ↓ *T. trichiura*
	Temperature	Population	−0.062	0.023	7.414	0.007	↑ temperature ↓ *T. trichiura*
Strongyles[c]	*T. trichiura*	Individual	0.746	0.142	25.223	0.000	↑ *T. trichiura* ↑ strongyles
	Group size	Group	−0.012	0.005	5.564	0.023	↑ group size ↓ *strongyles*
A. caucasica[d]	*S. pigmentatus*	Individual	0.669	0.223	3.628	0.002	↑ *S. pigmentatus* ↑ *A. caucasica*
	SCI to males	Individual	0.251	0.092	6.000	0.006	↑ connectedness ↑ *A. caucasica*
	Group size	Group	0.013	0.005	2.513	0.011	↑ group size ↑ *A. caucasica*
	Rainfall	Population	−0.083	0.014	40.105	0.000	↑ rainfall ↓ *A. caucasica*
S. pigmentatus[e]	*A. caucasica*	Individual	0.597	0.216	4.574	0.006	↑ *A. caucasica* ↑ *S. pigmentatus*
	Rainfall	Population	0.038	0.014	8.009	0.007	↑ rainfall ↓ *S. pigmentatus*
Parasite[f] richness	SCI 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

Note: Abbreviation: SCI: Social connectedness index.

[a] Random effects were female identity and identity of person who counted the parasites (observer). The standard deviation (σ), percentages of variance explained (% of σ^2) and *p*-values for random effects in each model are given below (from ranova in *lmerTest*, Kuznetsova et al., 2016).

[b] Female identity (σ = 0.35; % of σ^2 = 26.8%; *p*-value < 0.001); observer (σ = 0.13; % of σ^2 = 3.6%; *p*-value < 0.001); residual (σ = 0.57; % σ^2 = 69.6%).

[c] Female identity (σ = 0.95; % of σ^2 = 21.0%; *p*-value < 0.001); observer (σ = 0.31; % of σ^2 = 2.2%; *p*-value = 0.19); residual (σ = 1.81; % of σ^2 = 76.8%).

[d] Female identity (σ = 0.83, % of σ^2 = 16.4%; *p*-value < 0.001); observer (σ = 0.42; % of σ^2 = 4.3%; *p*-value < 0.001); residual (σ = 1.83 (% of σ^2 = 79.3%).

[e] Female identity (σ = 0.72; % of σ^2 = 11.5%; *p*-value < 0.001); observer (σ = 0.83; % of σ^2 = 15.3%; *p*-value < 0.001); residual (σ = 1.81; % of σ^2 = 73.2%).

[f] Female identity (σ = 0.39, % of σ^2 = 14.7%; *p*-value < 0.001); observer (σ = 0.28; % of σ^2 = 7.9%; *p*-value < 0.001); residual (σ = 0.89; % of σ^2 = 77.4%).

ecto-parasites sometimes increases female reproductive success (Hillegass et al., 2010; Neuhaus, 2003; Patterson & 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, Muñiz-Hernández, Hernández-Bello, & Morales-Montor, 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 IBIs, *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, Roberts, Carrero, & Morales-Montor, 2005; Hernández-Bello et al., 2010; Klein, 2000; Romano, Jiménez, Miranda-Brito, & Valdez, 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 GCs is often complex in natural populations, but a handful of other studies in primates have also reported positive associations between host GCs and helminth burdens (Arlet et al., 2015; Muehlenbein & Watts,

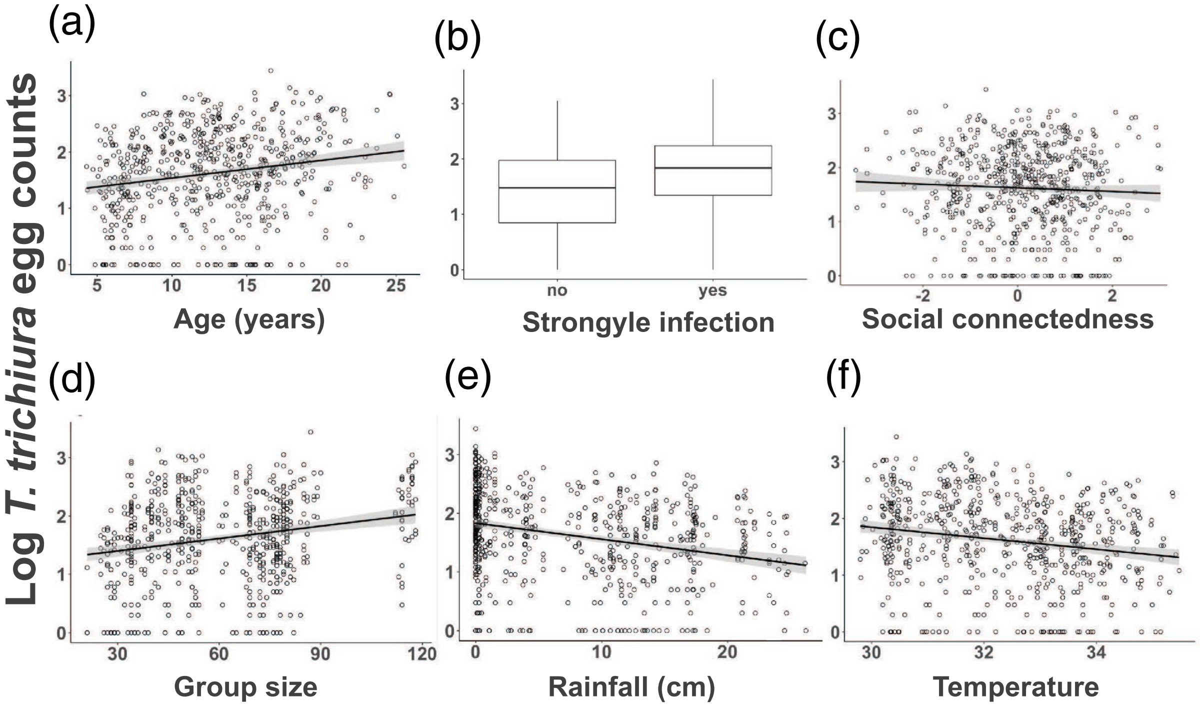


FIGURE 3 Association between log *Trichuris trichiura* egg counts and (a) presence/absence of strongyle infection; (b) female social connectedness to adult males; (c) age in years; (d) group size; (e) rainfall in the previous 3 months (cm); (f) average maximum temperature in the previous 3 months

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 co-infection. In particular, we found positive associations between three pairs of parasites (a) *T. trichiura* and strongyles, (b) *A. caucasica* and *S. pigmentatus and* (c) *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 faecal–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 & 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, Smith, & Layton, 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 trade-offs 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 immunosenescence (Nunn & Altizer, 2006; Wilson et al., 2002). Disentangling the effects of exposure and immunosenescence on worm burden is challenging in wild populations. Adult *T. trichiura* are thought to live for 1–2 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 & Poulin, 1995; Patterson & 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 faecal contamination in the environment; hence, members of larger groups may live at higher social densities and encounter faecal contamination from group members more frequently than baboons living in smaller groups. While strongyles are also transmitted via faecal–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 & 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 & Altizer, 2011; Koski & Scott, 2001; Martin, Weil, & Nelson, 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 & 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 multiscale 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 sample sizes and to control for the probability of intermittent shedding of faecal eggs.

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AUTHORS' CONTRIBUTIONS

M.Y.A., D.J., S.C.A., B.H. and E.A.A. designed the study; M.Y.A., B.H., L.G., S.C.A. and E.A.A. collected data; M.Y.A. and D.J. analysed the data; M.Y.A., S.C.A. and E.A.A. 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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