



Logging effects on parasitic infections in a swamp rat (*Malacomys edwardsi*) in West Africa

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Habitat disturbance can have negative impacts on biodiversity, such as reducing species richness. The effects of habitat disturbances on parasite infections of host species, potentially altering their survival rate and thus abundance, are less well known. We examined the influence of forest logging in combination with seasonality, host abundance, host body condition, and host sex, on the community composition of gastrointestinal parasites infecting Edward's swamp rat, *Malacomys edwardsi*. Community composition of parasites did not differ between logged and undisturbed sites, but the abundance of some nematodes (i.e., *Ascaris* and hookworm) was higher in undisturbed than logged sites. The higher abundance of these nematode species implies a changed host-parasite relationship, thus potentially influencing host persistence.

Key words: chainsaw milling, Ghana, helminths, host–parasite relationships, multiparasitism, small mammal, tropical forest

Habitat disturbances have the potential to change the abundance and distribution of wildlife. Changes in abundance in particular are the result of an alteration in the reproductive success and the survival of individuals (Safina and Burger 1983; Gill et al. 1996; French et al. 2011). One proxy to estimate how likely individuals are to survive and reproduce is the degree to which individuals are infected with parasites. Individuals are infected by a diversity of endoparasites in the gastrointestinal system, infections that can result in any one of many pathological effects, with some impacts being subclinical and others more evident (Holmes 1987; Gunn and Irvine 2003; Cripps et al. 2014). For example, hookworm infections can cause anemia, retard growth, and result in tissue damage and eventual mortality of their hosts (Seguel and Gottdenker 2017).

Parasite communities are structured by a combination of different processes such as dispersal events and ecological selection. Dispersal events describe how parasite species colonize and reach the host among and within habitat patches (Guégan et al. 2005) while ecological selection refers to biotic and abiotic filter factors that determine which parasites

persist in a habitat; i.e., host traits, interactions among parasite species, and habitat disturbance (Belyea and Lancaster 1999; Vellend 2010; Chase and Myers 2011). Host traits such as sex (i.e., hormonal and behavioral differences) and body condition also influence host susceptibility to parasite infection (Brunner et al. 2014; Luguterah and Lawer 2015; Oliver-Guimerá et al. 2017; Kołodziej-Sobocińska et al. 2018; Segura et al. 2019) and are linked to the immune system (Zuk and McKean 1996; Abolins et al. 2018). Interactions among multiple parasite species within a host can lead to trait-based competitive exclusion or facilitation of parasites (Graham 2008; Rynkiewicz et al. 2015). Furthermore, parasite species may not occur in a habitat because they are incompatible with abiotic factors (e.g., temperature, humidity) that were altered by anthropogenic activities (Kelley 1980; Lafferty and Kuris 1999; Friedman and Lawrence 2002). Thus, ecological selection and dispersal jointly can drive the abundance and diversity of parasites.

In tropical forests across the world, anthropogenic activities such as logging and agriculture occur at alarming rates (Benhin 2006). In Africa, exploitation of forests is expected

to increase with human population growth (Guariguata et al. 2010; Suleiman et al. 2017). In Ghana for instance, agriculture, logging, and mining present challenges for forest protection and management efforts (Schueler et al. 2011; Acheampong et al. 2019; Tsai et al. 2019). In particular, chainsaw milling is widespread in tropical forests, is often carried out illegally, and entails the selective removal of trees and their onsite conversion to lumber (Wit and van Dam 2010). The practice has gained popularity due to its low operational and investment costs. Although this activity sometimes is legal in many tropical developing countries (Marfo 2010; Kishor and Lescuyer 2012), it is not adequately regulated and could disrupt host-parasite interactions by altering the exposure of hosts to parasites by the processes of ecological selection and dispersal events.

There is evidence that anthropogenic activities have negative effects on forests and increase parasite or disease transmission, particularly in zoonotic infections in villages and towns on the periphery of forests (Gillespie et al. 2005; Wright et al. 2009; Wilkinson et al. 2018; Brock et al. 2019; Olivero et al. 2019). However, little is known about regular small-scale impacts, such as the effects of chainsaw milling on parasitism patterns in small mammal populations; we therefore address the following questions by evaluating endoparasites in Edward's swamp rat, *Malacomys edwardsi*. First: how does logging in the form of chainsaw milling influence the community composition of gastrointestinal parasites and hence the co-occurrence of parasites in hosts? Second: what determines the rate of parasite infection of individual swamp rats? Here, we hypothesized that differences in habitat disturbance (logged vs. undisturbed), season (dry vs. wet), and host abundance and traits (sex, body condition) will result in differences in parasite abundance.

MATERIALS AND METHODS

Study area and sites.—The study was undertaken in Atewa, an upland evergreen forest located within the high forest zone of Ghana (highest peak is 842 masl; Hall and Swaine 1981) that is comprised of two forest blocks: the Atewa Range (237 km²) and the Atewa Range Extension (21.3 km²). Our study occurred in the larger forest block, the Atewa Range Forest Reserve (Fig. 1). The forest has a bimodal rainfall pattern annually with an average annual precipitation of about 1,650 mm. Major and minor wet seasons occur from May to July and September to October/November respectively. Lower temperatures and higher rainfall often are recorded in the wet than in the dry season (Supplementary Data SD1). The forest is biologically diverse in flora and fauna with several rare and endemic species, such as the Atewa dotted butterfly (*Mylothris atewa*), the ursine colobus monkey (*Colobus vellerosus*), and the large-headed shrew (*Crocidura grandiceps*; McCullough et al. 2007). Large parts of the forest are intact, but chainsaw milling, hunting, and agriculture nevertheless occur. Besides its rich biodiversity, portions of the reserve have significant gold and bauxite deposits, drawing the interests of international mining companies as well as illegal artisanal and small-scale miners (Kusimi 2015).

We collected data in five logged (chainsaw milled-CM) and five undisturbed (UF) sites within the Atewa Range Forest Reserve in the wet (1 July—5 August) season and increased it to 12 (6 CM, 6 UF) in the dry season (8 November—19 December) of 2018. These sites were spread across the three locations (i.e., towns) of Asiakwa, Kibi Apapam, and Segyimase. Sites were chosen based on the absence or presence of logging disturbance within the forest. Investigated chainsaw-milled sites had logging intensities of two to seven trees of various diameters at breast height per site (~1 ha) and the lumber was transported out of the forest without using machinery. Canopy cover was higher in undisturbed than in logged sites (% $\bar{x} \pm SE$; CM = 48.2 \pm 9.7, UF = 93.3 \pm 1.3).

Live-trapping and quantification of fecal parasites.—A total of 25 Sherman traps (7.62 cm \times 8.89 cm \times 22.86 cm) arranged in a 5 \times 5 array and separated by a distance of 10 m were placed at each site. Traps at each site were active for three consecutive nights per sampling session with arrays left unchanged during sessions (i.e., seasons). All traps were placed at ground level, preferably at places that provided cover for small mammals (e.g., downed wood and rocks). Traps were baited with peanut butter mixed with oat, corn, and dried fish. Baited traps were set before sunset on the first day. They then were left opened for the duration of each trapping session per site and checked daily between 6 a.m. to 9 a.m. for captures. The survey yielded a sampling effort of 1,650 trap nights. Trapping and handling of animals conformed with the guidelines of the American Society of Mammalogists (Sikes et al. 2016). Animals captured for the first time were marked using ear tags with unique codes to allow for identification of recaptures (National Band and Tag Company, Newport, Kentucky). Individuals were identified to species level using identification guides (Grubb et al. 1998; Kingdon et al. 2013; Monadjem et al. 2015), sex was determined, and measurements taken (weight, head and body length, and hind foot length). Traps were inspected for scat samples which were immediately preserved in formol ether.

To examine gastrointestinal parasite abundance, we used the formol-ether sedimentation method to concentrate scat parasites (Uga et al. 2010) which then were stained on a microscopic slide and observed under 100 \times and 400 \times magnification with a compound light microscope for the identification of parasites using morphological keys (Ash et al. 1994). The detection and identification of parasites were based on egg, cyst, and larvae morphology (Supplementary Data SD2). The number of each parasite species was counted to obtain their respective abundances per scat sample (i.e., host individual).

While we trapped a total of six small mammal species (Supplementary Data SD2) we used the swamp rat *M. edwardsi* as study organism because it was found to be the most abundant species in the study area (Lawer et al. 2021). This small mammal species lives in primary forests but also can inhabit disturbed or secondary forest sites (Happold 2013). The genus *Malacomys* is known to be commonly infected by nematodes and mites among other parasites (Pearse 1929; Sakka and Durette-Desset 1988; Bochkov and Fain 1997; Bain and Junker 2013).

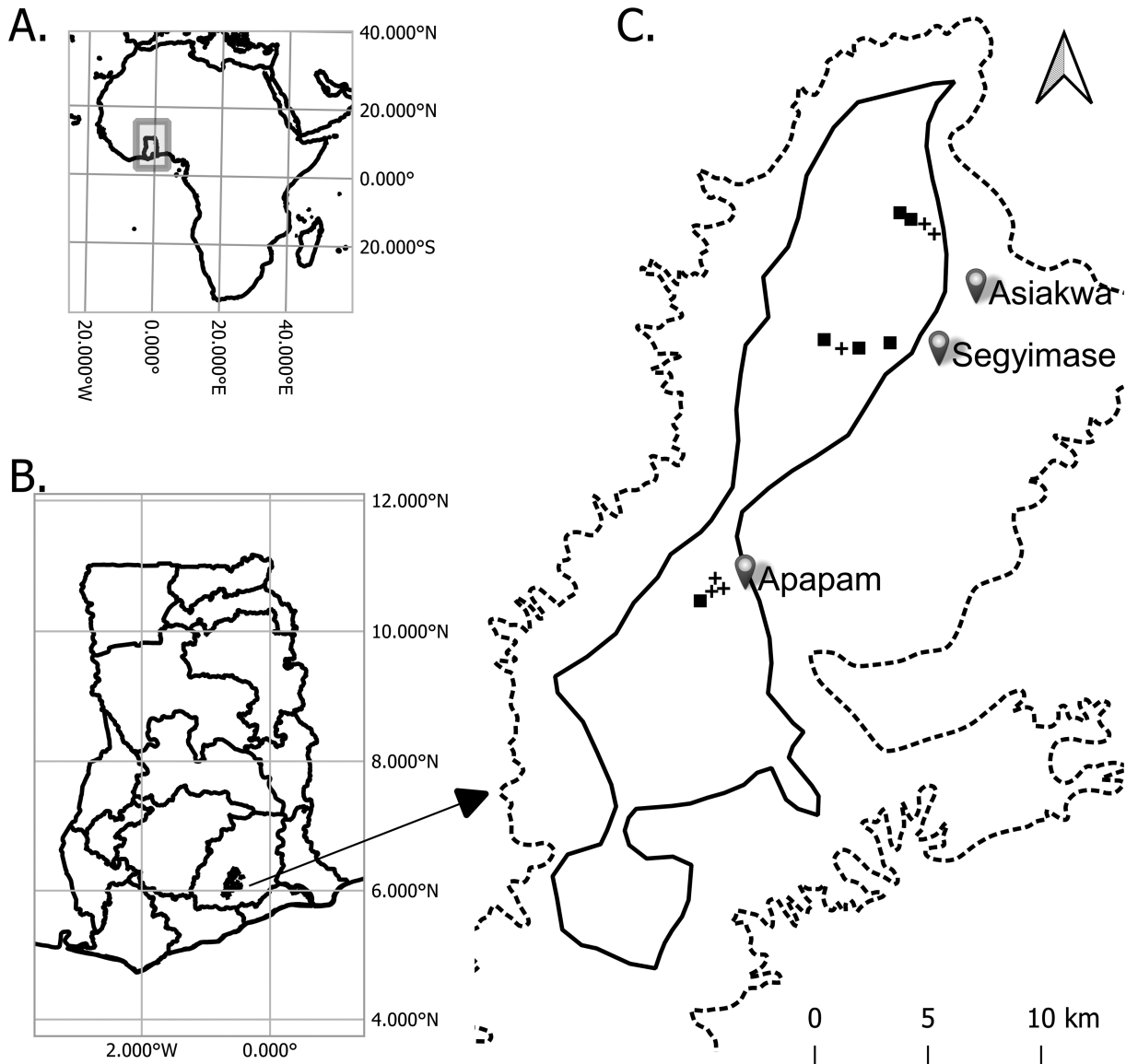


Fig. 1.—Map of the study area: (A) Africa, (B) Ghana, and (C) Atewa forest reserve showing sampled sites for small mammals from July to December 2018. The dotted line in C shows the Atewa mountain range while the solid line represents the forest reserve. Undisturbed sites are denoted by filled squares while logged (i.e., chainsaw milled) sites are represented by filled crosses.

Co-occurrence and community composition analyses.—All statistical analyses were undertaken in the program R (R Core Team 2020). To identify the co-occurrence patterns in parasite communities, i.e., whether two parasites frequently occurred together or avoided each other, pairwise ecological relationships among gastrointestinal parasites were quantified using the probabilistic model of species co-occurrence on presence-absence data implemented in the *cooccur* package (Veech 2013; Griffith et al. 2016). The model calculates the observed and expected frequencies of co-occurrence between each pair of species. The expected frequency is based on a random distribution of each species, independent of the other species. Probabilities returned from the analysis indicate that two species would co-occur more or less frequently than observed at an alpha threshold of 0.05: species pairs then are classified as having positive (species co-occur significantly more frequently

than expected), negative (species co-occur significantly less frequently than expected) or random (observed frequency of co-occurrence does not significantly differ from expected) associations.

To analyze differences in the community composition, we visualized the Bray–Curtis dissimilarity in parasite communities with non-metric multidimensional scaling (NMDS) using the *vegan* package’s function *metaMDS* (Oksanen et al. 2019). Effects of forest disturbance and season on the parasite communities were analyzed using permutational multivariate analysis of variance while controlling for site-level variation based on location of site (PERMANOVA, *vegan* package, function *adonis*).

Parasite count analysis.—One of the predictors included in the model to describe parasite abundance was the scaled mass index (SMI), i.e., a measure of the hosts’ body condition

(Peig and Green 2009). This approach takes into account the scaling relationship between body mass and a distinct linear body measurement according to the equation: $SMI = M_i(L_0/L_i)^{bSMA}$, where M_i and L_i are the respective body mass and size of the i th host individual; L_0 is a predefined value of body size (taken as the arithmetic mean of body length in this study); and $bSMA$ is the scaling exponent calculated by standardized major axis regression. We used the $bSMA$ coefficient estimated for undisturbed (reference) sites to calculate the SMI for the entire data, as suggested by Peig and Green (2010). The “smatr” package was used for the estimation of the $bSMA$ coefficient (Warton et al. 2012).

Parasite count data as a proxy for the infection rate of small mammals were analyzed using generalized models. We used generalized linear mixed models (GLMM), hurdle models, and generalized additive mixed models (GAMM) in packages glmmTMB (Brooks et al. 2017) and mgcv (Wood 2017). Depending on the best model fit identified based on the Akaike information criteria (AIC; bml package, function AICtab; Bolker and Team 2017), Poisson, negative binomial, or zero inflated models for count data were selected. Models with an additive effect were included because body condition and parasite abundance do not always follow a linear (negative) relationship (Maceda-Veiga et al. 2016). Response variables in the models were abundance of total parasites, *Ascaris*, *Strongyloides*, and hookworm (includes multiple genera: e.g., *Necator* and *Ancylostoma*), with the following fixed predictor variables: disturbance (logged vs. undisturbed), season (dry vs. wet), sex, SMI (condition), and small mammal abundance. We used small mammal abundance per site as a proxy for population size of host. Location of sampling sites was

considered as a random variable in all tentative models. GAMM was selected for total, *Ascaris*, and hookworm, while GLMM was chosen for *Strongyloides* parasite count analyses (Supplementary Data SD3).

To verify model validity and check whether co-linear predictors would cause harm, we carried out two tests. The variance inflation factor (VIF; for GAMMs, mgcv.helper was used; Clifford 2019) was calculated and explanatory variables with VIFs greater than 5 subsequently were excluded from models (Supplementary Data SD3). VIF values <5 in final models indicated an absence of multicollinearity (Kutner 2005). In addition, residual diagnostics of models using the DHARMA package (Hartig 2019) suggested that selected models were adequate and fit the data well (Supplementary Data SD4).

Low sample size may lead to a weak statistical power. We approximated the power of our mixed model analysis by estimating the power of a corresponding generalized linear mixed model with Poisson distribution (R package “simr”; Green and MacLeod 2016).

RESULTS

Nineteen of 32 trapped rats were infected by gastrointestinal parasites. Parasites belonged to 12 taxonomic groups (species of helminths and protozoans; CM = 6, UF = 11; Fig. 2). *Ascaris* species were the most abundant parasite group, infecting about 38% of hosts (12/32). The next most dominant parasite groups were species of hookworms and *Strongyloides*, infecting approximately 25% of all hosts (8/32). Two protozoans, *Trichuris trichiura* and *Giardia* sp., were found only in undisturbed sites, but with low infestation (abundance) and

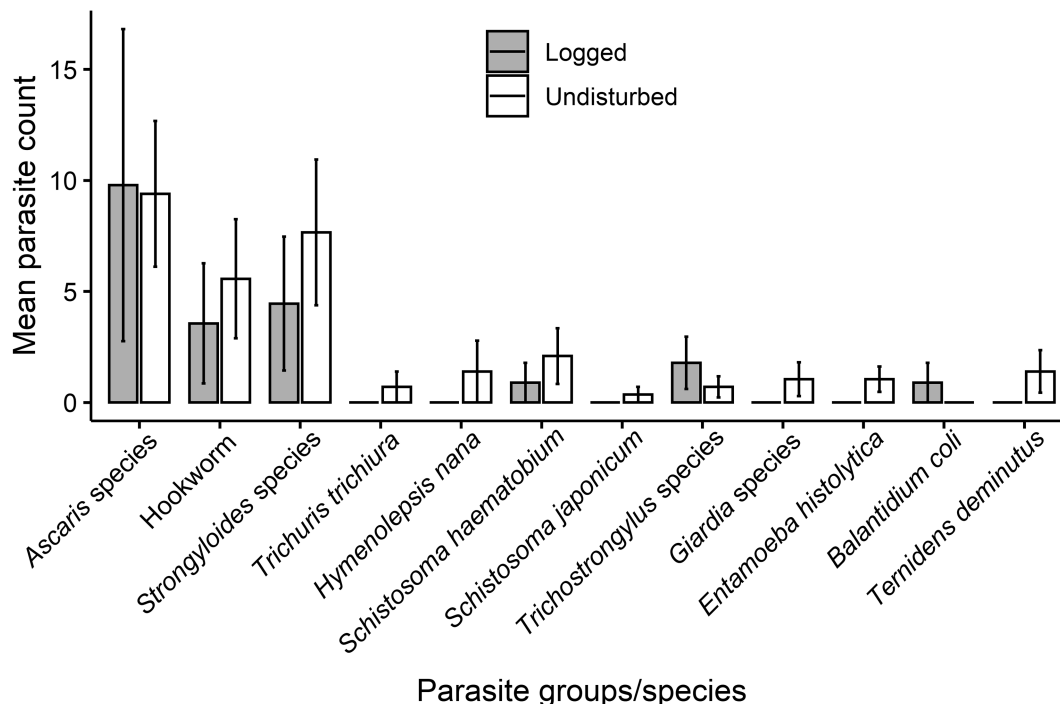


Fig. 2.—Mean ($\pm SE$) parasite taxonomic abundance per host individual (Edward’s swamp rat, $n = 32$) in logged and undisturbed sites in Atewa range forest reserve, July to December 2018.

prevalence (<7%; Fig. 2). Prevalence of parasites did not differ by habitat disturbance ($P = 0.427$), season ($P = 0.721$), and sex ($P = 0.070$), based on the results of a Fisher's exact test.

Parasite species co-occurrence and community composition.—We pooled all data for the co-occurrence analysis. Our probabilistic analyses of parasite species co-occurrence revealed instances of only positive and random species associations (no negative associations; Fig. 3). Approximately 8% of species pair associations were positive (nonrandom) while the remaining 92% were random: hookworms in particular accounted for more of the positive associations (more frequent in combination with nematode species). This indicates that the species composition of parasite communities predominantly followed random patterns of community assembly.

In addition, non-metric multidimensional scaling plots revealed lack of clustering of parasites by disturbance and season (Fig. 4). Permutational multivariate analyses of variance confirmed that both disturbance (d.f. = 1, $F = 0.115$, $P = 0.996$) and season (d.f. = 1, $F = 0.937$, $P = 0.545$) had no significant effects on gastrointestinal parasite composition.

Disturbance, season, and host traits as predictors of parasite abundance.—Disturbance, season, and host characteristics

significantly influenced *Ascaris* and hookworm abundances, except for total abundances of parasite and *Strongyloides* (Table 1). In particular, we found that female swamp rats on average had significantly higher *Ascaris* and hookworm abundance than males (Fig. 5). Hosts inhabiting undisturbed sites had higher parasite abundances than logged sites. In terms of seasonality, *Ascaris* and hookworm infections were respectively high in the wet and dry seasons (Fig. 5). Small mammal abundance used as a proxy for population size was positively correlated with abundance of *Ascaris* (Supplementary Data SD5). We found a significant non-linear effect of body condition on *Ascaris* abundance (Table 1, *Ascaris* model): i.e., *Ascaris* abundance likely peaks at intermediate body condition (Supplementary Data SD5). We observed a different trend (linear) for hookworms however, where hosts with lower body conditions were less infected than hosts with higher body conditions (Supplementary Data SD5). The estimated power for the model parameters based on our sample size of 32 appeared to be sufficient in most cases. Only the disturbance parameter in the model for *Strongyloides* had a low power (8%); all other parameters in the fitted models had sufficient power, ranging from 35% to 95% (Supplementary Data SD4).

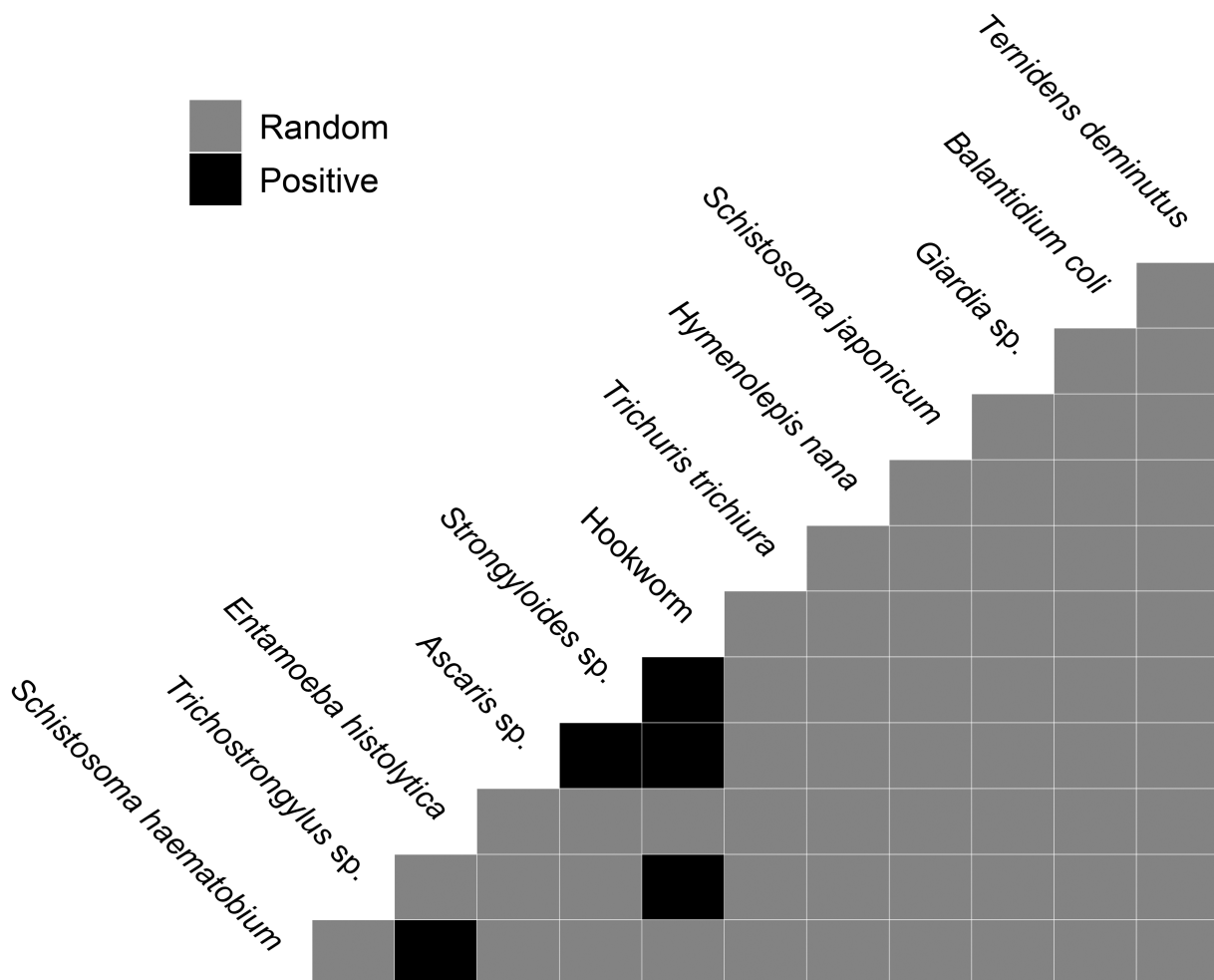


Fig. 3.—Pairwise co-occurrence patterns between gastrointestinal parasites infecting Edward's swamp rat in Atewa range forest reserve, July to December 2018.

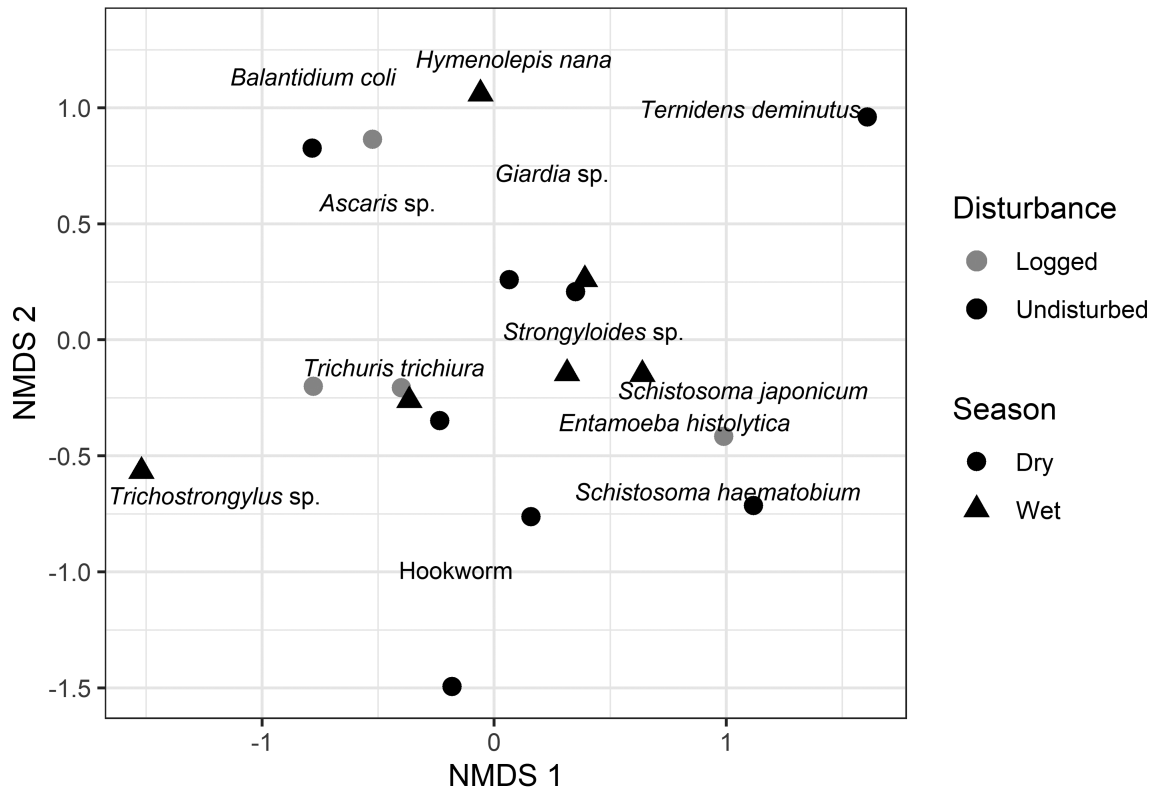


Fig. 4.—Non-metric multidimensional scaling plot of parasite composition based on Bray–Curtis dissimilarity on abundance data ($k = 3$, stress = 0.062) from Atewa range forest reserve survey (July to December 2018). There are no logged sites for the wet season in the figure, because host individuals (Edward’s swamp rat) sampled in the logged sites during the wet season had no gastrointestinal parasite infections.

Table 1.—Results of model comparison predicting parasite abundances in *Malacomys edwardsi* starting with a full model including all predictors: disturbance (logged vs. undisturbed), season (dry vs. wet), and host traits (sex, small mammal abundance-TSMA, and scaled mass index-SMI) with location set as a random variable. Rows with an “a” superscript indicate that a smooth (thin-plate regression spline) was applied to the predictor variable of that specific model and its respective degrees of freedom (d.f.) are actually the estimated degrees of freedom (e.d.f.). Final/reduced model outputs are presented in Fig. 5 and Supplementary Data SD5 (or see Supplementary Data SD6 for parameter estimates). Results are based on a sampling period from July to December 2018 in the Atewa range forest reserve.

Variable	Total parasites			<i>Ascaris</i>			<i>Strongyloides</i>			Hookworms		
	d.f.	χ^2	<i>P</i>	d.f.	χ^2	<i>P</i>	d.f.	χ^2	<i>P</i>	d.f.	χ^2	<i>P</i>
Disturbance	1	0.029	0.866	1	11.46	0.0007	1	0.020	0.90	1	38.929	<0.0001
Season	1	0.282	0.595	1	11.69	0.0006	1	0.330	0.57	1	42.111	<0.0001
Sex	1	1.023	0.312	1	29.88	<0.0001	1	0.840	0.36	1	47.146	<0.0001
TSMA	1	0.100	0.752	1	40.330	<0.0001	1	0.300	0.58	1	0.788	0.375
SMI	1.036 ^a	0.202 ^a	0.7012 ^a	7.564 ^a	304.208 ^a	<0.0001 ^a	1	0.310	0.58	1 ^a	329.610 ^a	<0.0001 ^a

DISCUSSION

Parasite communities vary across space and time, and among populations (Gotelli and Rohde 2002). The similarity in parasite community composition between logged and undisturbed sites likely is due to the relatively low disturbance levels associated with logged sites (i.e., despite differences in parasite occurrence and abundance; Lawer et al. 2021). Indeed, when pooling data, our results suggest that parasite communities were shaped by predominantly random patterns of species co-occurrence. This can be attributed to the lack of interspecific interactions among parasite groups, a pattern that similarly was observed in fishes (Gotelli and Rohde 2002), another mammal

species (Fellis et al. 2003), and arthropods (Adair et al. 2018). Alternatively, the composition of parasites in the host could reflect random encounters with infectious parasite stages in the environment.

Abundances of *Ascaris* and hookworms (but not *Strongyloides*) were significantly lower in logged compared to undisturbed sites, suggesting that different parasite groups respond differently to varying levels of habitat disturbance (Wolinska and King 2009; Carbayo et al. 2019). Similarly, seasonal variation in parasite abundance has been reported for other groups of hosts including small mammals (Wiger 1979; Raharivololona and Ganzhorn 2010; Viljoen et al. 2011; Archer et al. 2017). Climate and weather affect parasites differently

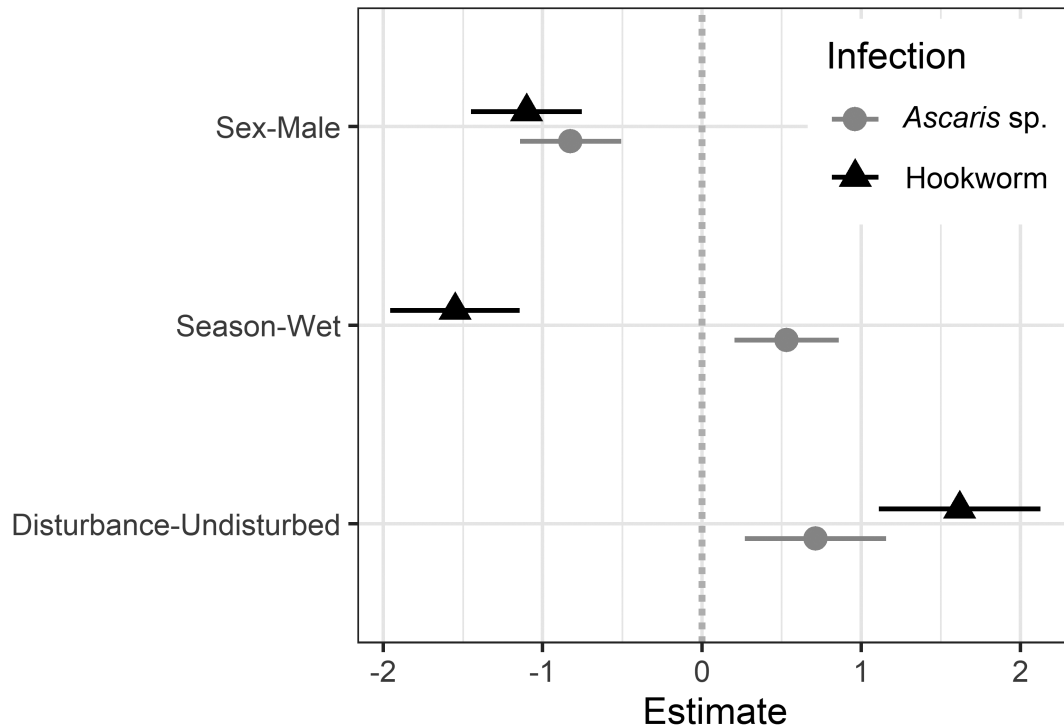


Fig. 5.—Response of parasite abundance to predictor variables based on final models (as in Supplementary Data SD6): shown only for significant categorical variables, namely, Sex (ref = Female), Season (ref = Dry) and Disturbance (ref = logged). Results are based on parasite data collected on Edward's swamp rat from Atewa range forest reserve, July to December 2018.

due to their varying life histories and optimum meteorological requirements (temperature, humidity/rainfall). For instance, the infective L3 stage of bursate nematodes (order Strongylida: hookworms) migrate onto vegetation and are more directly impacted by meteorological factors such as erratic rainfall than their earlier life stages (eggs and L1 and L2 stages still live in the feces; Levine 1980). Unlike bursate nematodes, the eggs of *Ascaris* species (order Ascaridida) can remain alive and infective for long periods under varying stress levels (≤ 5 years under field and laboratory conditions; Brown 1928). This may have accounted for the decreased hookworm abundance in the wet season, while *Ascaris* were more abundant. We also do not rule out the effect of parasite biology (life cycle) in the patterns observed for *Strongyloides*. For example, the autoinfection ability of *S. stercoralis* (Viney and Lok 2007) could have accounted for the observed patterns due to multiple reinfections within hosts. Also, free-living infective filariform (L3 stage) larvae of *S. ratti* (a parasite of rats) are long lived and can persist in an environment until a suitable host is found (Viney and Lok 2007). Although we did not distinguish between species of *Strongyloides* in our analyses, and given the life cycle of rhabditid nematodes which alternate between free-living and parasitic forms, further research is required to assess the generality of the observed patterns across other host taxa.

Host ecology and traits including population size, sex, and body condition can affect parasite infection intensities. Population size of swamp rats affected *Ascaris* abundance, suggesting that abundant populations of small mammals increase encounter rates and contact with fecal matter, thus enhancing parasite transmission (Anderson and May 1979; Stenkewitz

et al. 2016; Sugiura et al. 2018). In our study, female swamp rats were more infected than males both by *Ascaris* and hookworms. Although this finding is not surprising (Lloyd 1983; Sanchez et al. 2011), countless studies have reported contrary results (Oliver-Guimerá et al. 2017; Segura et al. 2019). In rodents for example, an absence of sex-biased parasitism (Čabrilo et al. 2018) and the presence of female- and male-biased parasitism (Krasnov et al. 2005) have been recorded, suggesting a complex phenomenon mediated by several mechanisms (e.g., physiology, behavior). Host species variation in trade-offs between sexually selected traits and immune function could be an explanation for differences in sex-biased parasitism (Sheldon and Verhulst 1996; Hosken and O'Shea 2001; Hillegass et al. 2008). Likewise, body condition can have a significant effect on parasite abundance. Exploratory tests revealed non-significant differences in body condition related to logging, season, and sex (Supplementary Data SD5). If body condition is tightly linked with immune defense (Abolins et al. 2018), and body condition does not vary based on disturbance, season, and sex, then it is likely that total parasite abundance will not vary for these variables due to similarity in immunity. For instance, Winternitz et al. (2012) found no relationship between host condition and parasites. However, species co-occurrence patterns especially among nematodes could have accounted for the relationships in the two taxonomic groups due to facilitation (Graham 2008)—i.e., linear relationship for hookworm and non-linear relationship for *Ascaris* (Supplementary Data SD5). We found that nematode species co-occurred more frequently than expected. Positive species associations may arise through mutualistic interactions between phylogenetically distant taxa

(Zelezniak et al. 2015; Rakoff-Nahoum et al. 2016), or when one species facilitates the other via host immunosuppression by the first arriving parasite (Lello et al. 2004; Graham 2008). Notably, our findings highlight that linear negative relationships between parasite abundance and body condition are not universal (Maceda-Veiga et al. 2016).

Another factor that may explain the observed patterns in parasite abundance and community composition is patch connectivity (Altermatt and Holyoak 2012; Spiesman et al. 2018; Santos et al. 2019). Timber exploitation by chainsaw milling is widespread in the reserve (Asamoah et al. 2011), creating patches of undisturbed forest with animals moving among patches. Random encounters between hosts and parasites therefore may be another factor driving the parasite community composition within the forest (because patches are not isolated). Since infection intensity was high in undisturbed sites (and small mammal abundance was relatively high in undisturbed forests; Lawer et al. 2021), hosts may have been releasing large numbers of parasite eggs in feces into the environment. This could have increased the likelihood of contact with infected fecal matter by hosts, leading to more infections in undisturbed sites. Alternatively, the decline in infections in logged sites may be due to a disruption in the life cycle or development of some parasite species outside the host in disturbed habitats (Gardner and Campbell 1992; Cardoso et al. 2016; Boundenga et al. 2018; Galbreath et al. 2019).

For both logged and undisturbed sites, parasite communities were shaped predominantly by random patterns of species co-occurrence. Contrary to expectations, some taxon-specific group abundances were significantly lower in logged compared to undisturbed sites. We acknowledge the potential limitation posed by our small sample sizes and the likely impact this could have on parameter estimates. Power analysis of corresponding GLMMs suggested a sufficiently large sample size to run our models (Supplementary Data SD4), but we nevertheless advise for future studies to increase the sample sizes to verify our findings. That stated, our results suggest the possible effect of logging on host-parasite relationships for at least some parasites of the swamp rat.

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CONFLICT OF INTEREST

None declared.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Plot of meteorological variables of the study region.

Supplementary Data SD2.—List of captured small mammal species and images of gastrointestinal parasites observed during laboratory analysis.

Supplementary Data SD3.—Model comparisons and VIF of selected models.

Supplementary Data SD4.—Residual diagnostics of final models and power analysis of corresponding GLMMs.

Supplementary Data SD5.—Visualization of fitted final models and box plots of SMI.

Supplementary Data SD6.—Parameter estimates and standard errors of final models.

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