Effects of anthropogenic and demographic factors on patterns of parasitism in African small mammal communities

JOHANNA S. SALZER[1,2,3], DARIN S. CARROLL[2,3], AMANDA JO WILLIAMS-NEWKIRK[1,2,4], STEFANIE LANG[2], JULIAN KERBIS PETERHANS[5,6], INNOCENT B. RWEGO[2,7,8], SANDRA OCKERS[7] *and* THOMAS R. GILLESPIE[1,2,7]*

[1] *Program in Population Biology, Ecology, and Evolution, Emory University, 1462 Clifton Road, Atlanta, Georgia 30322, USA*
[2] *Department of Environmental Sciences, Emory University, 400 Dowman Drive, Atlanta, Georgia 30322, USA*
[3] *Poxvirus and Rabies Branch, Division of High-Consequence Pathogens and Pathology, Centers for Disease Control and Prevention, 1600 Clifton Road, Atlanta, Georgia 30333, USA*
[4] *Rickettsial Zoonoses Branch, Division of Vector-borne Diseases, Centers for Disease Control and Prevention, 1600 Clifton Road, Atlanta, Georgia 30333, USA*
[5] *College of Professional Studies, Roosevelt University, 430 South Michigan Avenue, Chicago, Illinois 60605, USA*
[6] *Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA*
[7] *Department of Environmental Health, Rollins School of Public Health, Emory University, 1518 Clifton Road, Atlanta, Georgia 30322, USA*
[8] *Department of Biological Sciences, Makerere University, Kampala, Uganda*

(*Received 16 August 2013; revised 10 August 2014; accepted 13 August 2014; first published online 29 September 2014*)

SUMMARY

Habitat disturbance often results in alterations in community structure of small mammals. Additionally, the parasites harboured by these small mammals may be impacted by environmental changes or indirectly affected by changes in available hosts. To improve our understanding of this interplay, we examined the patterns of parasitism in small mammal communities from a variety of habitats in forested Uganda. Small mammals were collected from areas experiencing variable habitat disturbance, host density and species richness. The analysis focused on 3 most abundant rodent species, *Lophuromys aquilus, Praomys jacksoni* and *Hylomyscus stella*, and a diverse group of parasites they harbour. The impact of various habitat and host community factors on parasite prevalence was examined using linear regression and Spearman's rank-order correlation. We further investigated the parasite communities associated with each individual using correspondence analysis. We determined that, parasite prevalence and richness may be occasionally influenced by community and habitat factors, but taxonomy is a driving force in influencing the parasite community harboured by an individual host. Ultimately, applying general principles across a broad range of disturbance levels and diverse host communities needs to be approached with caution in complex communities.

Key words: ectoparasites, fleas, *Giardia*, Kibale National Park, lice, mites, *Praomys*, rodent, ticks, trypanosome.

INTRODUCTION

Habitat quality, host community assemblage, host susceptibility/resistance and pathogen–pathogen interactions are interconnected in complex and dynamic ways (Woolhouse *et al*. 1997; Ostfeld *et al*. 2008; Beldomenico and Begon, 2010; Johnson *et al*. 2013). Disease dynamics can rarely be explained by examining one component of a complex natural system although general patterns are often sought. Understanding the host community components and interactions associated with disease emergence and persistence may provide valuable information for unlocking mechanisms driving disease dynamics in the natural environment (Dobson, 2004; Lafferty, 2010; Telfer *et al*. 2010).

Anthropogenic disturbance and subsequent loss of both biodiversity and community structure have been associated with increases in disease emergence (Keesing *et al*. 2010; Roche *et al*. 2012), as well as a reduction in disease occurrence (Lafferty, 2012; Bush *et al*. 2013; Young *et al*. 2013). There is evidence supporting both positive and negative general linear relationships among disease and factors such as diversity, density and relative abundance (Randolph and Dobson, 2012). Additionally, empirical evidence is mounting that a host species' relative abundance and density are also linearly associated with parasite prevalence and/or richness (Arneberg, 2002; Froeschke *et al*. 2013). Regardless of shape or direction and the indirect or direct influences, anthropogenic disturbance can affect disease dynamics in natural systems (Randolph and Dobson, 2012; Salkeld *et al*. 2013).

* Corresponding author. Program in Population Biology, Ecology, and Evolution, Emory University, 1462 Clifton Road, Atlanta, Georgia 30322, USA; Department of Environmental Sciences, Emory University, 400 Dowman Drive, Atlanta, Georgia 30322, USA; and Department of Environmental Health, Rollins School of Public Health, Emory University, 1518 Clifton Road, Atlanta, Georgia 30322, USA. E-mail: Thomas.Gillespie@emory.edu

Parasitology (2015), **142**, 512–522. © Cambridge University Press 2014
doi:10.1017/S0031182014001450

CrossMark

To improve our understanding of the general patterns between host and parasite communities in relation to anthropogenic disturbance, we investigated parasite dynamics in terrestrial small mammal communities in and around Kibale National Park (KNP), Western Uganda. Specifically, we focused on 3 common forest dwelling rodent species – *Lophuromys aquilus, Praomys jacksoni* and *Hylomyscus stella* (Delany, 1975; Struhsaker, 1997). We examined parasites of these host species and investigate correlations between parasite prevalence and habitat disturbance, host density and host species richness. We further evaluated the parasite communities harboured by each of these host species. These small mammals (or hosts) were collected from habitats experiencing variable intensities of habitat disturbance. The specific parasites investigated in our study included: gastrointestinal protozoans (*Giardia* spp. and *Cryptosporidium* spp.), blood-borne parasite (*Trypanosoma* spp.) and ectoparasites from the taxonomic orders Ixodida (ticks), Acarina (mites), Siphonaptera (fleas) and Phthiraptera (lice). This study investigates broad patterns pertaining to the relationships among parasite prevalence and community structure in habitats that vary by species richness, host density and disturbance intensity.

MATERIALS AND METHODS

Study area

KNP is a mid-elevation tropical moist forest located in the foothills of the Rwenzori Mountains in Western Uganda (0 13′–0 41′N, 30′19′–30′22′E) (Struhsaker, 1997; Chapman and Lambert, 2000; Hartter, 2009). The park and surrounding areas represent a mosaic of habitats that have undergone various types and frequency of habitat disturbance (Hartter, 2009). Portions of KNP were logged at varied intensities in the 1960s resulting in a series of contiguous forest compartments of lightly logged, heavily logged and unlogged status within KNP (Struhsaker, 1997). Over the last four decades KNP and the surrounding forest fragments have supported research on the influence of habitat disturbance on a variety of forest dwelling species (Kasenene, 1984; Isabirye-Basuta and Kasenene, 1987; Lwanga, 1994; Dranzoa, 1998; Chapman *et al*. 2000; Seavy and Apodaca, 2002; Gillespie and Chapman, 2008; Hartter *et al*. 2011). Our sampling sites represent a broad gradient of anthropogenic disturbance in the region, which was historically a contiguous forested area. Sampling sites included, from least to most disturbed: (1) relatively pristine forest (known as CC), (2) low-intensity selectively logged forest (known as K14), (3) high-intensity selectively logged forest (known as K15), (4) forest–agricultural interface (known as forest edge), (5) forest fragments (referred to as Fragments 1 and 2) and (6) human settlements (Fig. 1). All sites were sampled twice except for K15 and the forest edge. Previous studies within KNP (Chapman *et al*. 2000) and these forest fragments (Gillespie and Chapman, 2006) have extensively evaluated the gradient of habitat disturbance occurring in the areas studied in this investigation. These previous studies allow our specific study sites to be categorically placed along a gradient of disturbance (Gillespie *et al*. 2005; Gillespie and Chapman, 2006, 2008).

Animal collection

Trapping webs were used in all habitats except within village homes to accurately estimate the abundance, density and structure of the small mammal community within each habitat (Anderson *et al*. 1983). Each web was 200 m in diameter and covered 3·14 ha with 12 radii each containing 12 Sherman traps (3 × 3·5 × 9″, H.B. Sherman Traps, Inc, Tallahassee, FL), with the first 4 of these traps set at 5 m intervals and the 8 distal traps were set at 10 m intervals (Mills *et al*. 1999). The centre of the web contained 4 Sherman traps and 1 Tomahawk trap (19 × 6 × 6″, Tomahawk Live Trap Co., Tomahawk, WI). An additional 4 Tomahawk traps were each set 50 m from the centre in the cardinal directions. In total, 153 traps were used in each web. Trapping webs were operated for three consecutive nights on each trapping occasion for a total of 5049 trap nights at 7 sites. All sites were sampled on 2 occasions except the forest edge and heavily logged forest sites, which were sampled once. Traps were baited in evenings and animals were collected at sunrise the following morning to prevent trap-associated deaths. All traps were baited consistently with peanut butter and millet. All trapping was conducted in the dry season between May and July of 2009. Sites that had repeated sampling had at minimum a 6-week rest period between sampling efforts.

Terrestrial small mammal collection was approved by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, local authorities and homeowners at trap sites. Animal handling protocols were approved by Institutional Animal Care and Use Committees (IACUC) from Emory University (#062-2009) and the Centers for Disease Control and Prevention (CDC) (#1768).

Standard field methods for small mammal handling, necropsy and tissue collection techniques were followed (Mills *et al*. 1995). Necropsies were performed and tissue samples were collected for molecular identification of mammalian species and *Trypanosoma* spp. Feces were collected from the descending colon and preserved in 10% buffered formalin for detecting *Giardia* spp. and *Cryptosporidium* spp.. Skulls from a subset of small mammals sampled ($n = 137$) were prepared using standard procedures and identified to species using established

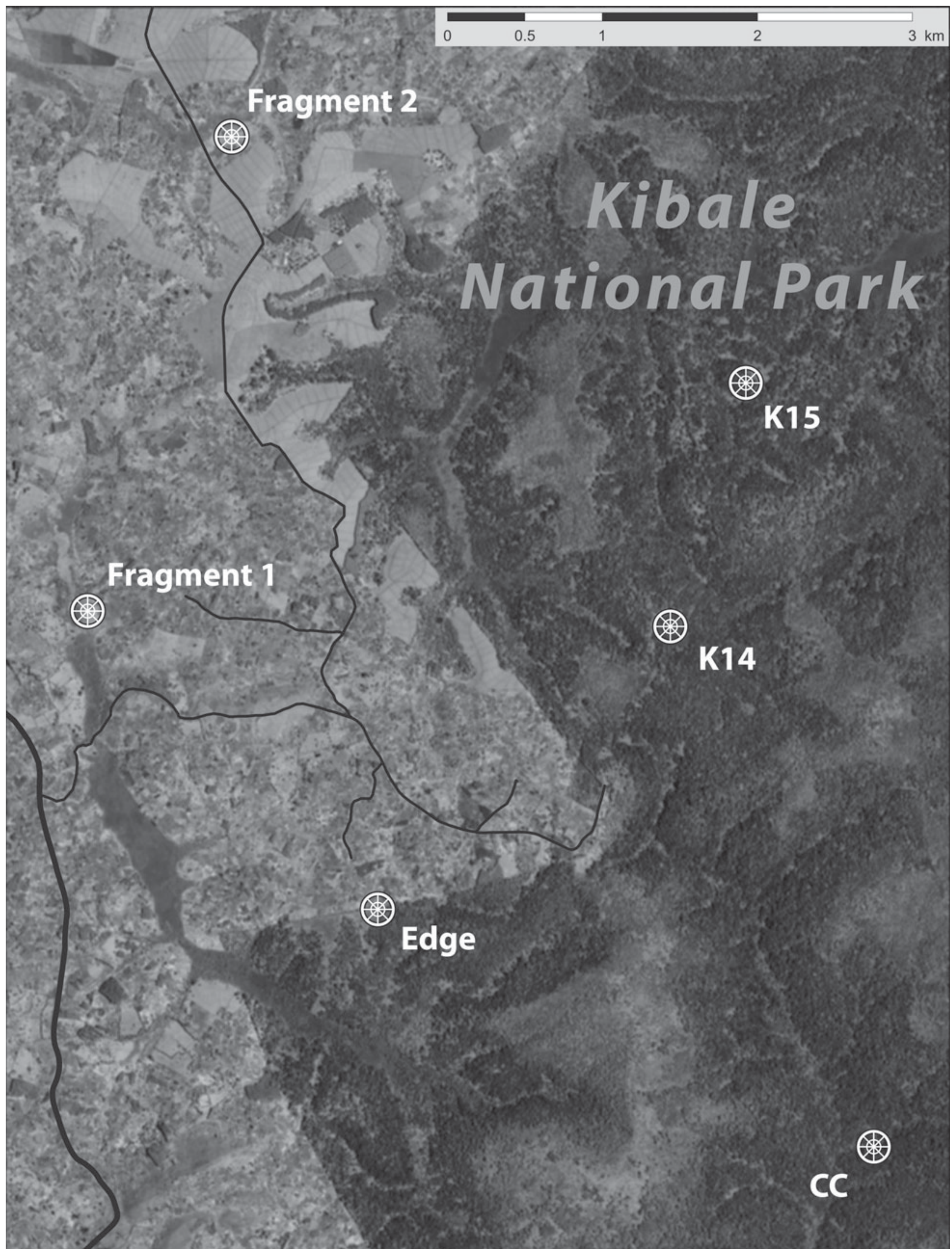

Fig. 1. Map of KNP (contrast enhanced as darker areas of image) and surrounding areas outside the national park. The area in the map was all once associated with a contiguous mid-elevation tropical moist forest. Specific locations of trapping webs (200 m in diameter) are identified as: *CC*, pristine primary forest; *K14*, lightly logged forest; *K15*, heavily logged forest; *Edge*, forest edge that overlaps agriculture fields; *Fragment 1*, located near the village of Bugembe and surrounded by small scale agriculture and human dwellings; *Fragment 2*, located near the village of Kiko and surround by small-scale agriculture, trading centre, and monoculture in the form of tea plantations. Small mammals were also collected from human dwellings located in areas around KNP and the forest fragments.

mammalian guides (Delany, 1975; Nagorsen and Peterson, 1980; Thorn and Kerbis Peterhans, 2009). Specimens were catalogued at the Field Museum in Chicago, IL, USA (Reference no. 210384–210540). Molecular identification using cytochrome B gene analysis was necessary for species indistinguishable by morphometrics (i.e. *P. jacksoni* and *P. misonnei*) (Peppers *et al*. 2002).

Immediately following humane euthanasia, each small mammal was placed in an individual plastic bag. The plastic bags containing euthanized small mammals were then opened and contents were placed in a clean white plastic tub (approximately 8 × 40 × 30 cm) (Bush, 2009). Each individual and the contents of their plastic bag were processed within the tub for easy visualization and collection of ectoparasites. Ectoparasites were dislodged and collected by vigorous brushing of euthanized small mammals. Attached ectoparasites (i.e. ixodid ticks) were collected by parting the fur of each individual animal with forceps and visually inspecting the skin. Small mammals were processed until no additional ectoparasites were collected or for a maximum of 20 min in the case of heavily infested animals and all ectoparasites were placed into 70% ethanol. This process was conducted to maintain consistency in collection methods.

Parasite detection

All parasites were identified to the level of order. DNA was extracted from the spleen tissue (stored at −80 °C) of all the animals collected ($n = 327$) using the DNA EZ1 tissue kit (Qiagen, Hilden, Germany). To detect *Trypanosoma* spp. DNA we amplified the highly variable region of the 18S ribosomal RNA gene using previously described nested PCR methods (Noyes *et al*. 1999) and Platinum Taq polymerase (Invitrogen, Grand Island, New York, USA). We used external primers TRY927F and TRY927R, and internal primers SSU561F and SSU561R to confirm Trypanosome-positive individuals (Noyes *et al*. 2002).

Formalin-preserved feces were screened for *Giardia* spp. cysts and *Cryptosporidium* spp. oocysts using the MERIFLUOR immuno-fluorescent assay (Meridian BioScience Inc. Cincinnati, Ohio, USA). Fecal samples were concentrated into fecal pellets and resuspended in 1 g/mL concentrations and scored for presence/absence (Salzer *et al*. 2007).

All ectoparasites were shipped to Emory University in Atlanta, Georgia, USA where they were examined by light microscopy. Ectoparasites from each animal were quantified and categorized according to taxonomic order – Ixodida (ticks), Acarina (mites), Siphonaptera (fleas) or Phthiraptera (lice) (Lane and Crosskey, 1993). Only motile stages were identified for each ectoparasite, including larval, nymphal and adult stages for ticks and mites; nymphal and adult stages for lice; and adult stage for fleas.

Data analysis

Relative small mammal density for each habitat was calculated and measured by trapping success divided by trapping effort for each habitat where trapping webs were used for animal collection (omitting human settlements from this analysis). Additionally, relative species abundance was measured by the number of total *L. aquilus, H. stella* and *P. jacksoni* divided by the total animals collected at each site. Using individual-based rarefaction, species richness was estimated for each habitat. A rarefaction curve was generated to determine adequate sampling effort and species richness to correct for varied sample sized across habitats.

Parasite point prevalence (referred to as prevalence) is the proportion of infected/infested individuals at the time of sample collection and was calculated for each habitat and the most abundant rodent species (*L. aquilus, H. stella* and *P. jacksoni*). Correlations between parasite prevalence and species richness, small mammal density and relative species abundance were measured using linear regression models with the prevalence of each parasite as outcome variable. Additionally, correlations between habitat disturbance and parasite prevalence were evaluated using Spearman's rank-order correlation, since habitat disturbance is a qualitative and ordinal variable. Statistical analyses were performed using the stats package on the R version 3.0.1 (R Core Team, 2013).

To determine if parasite assemblages were more influenced by habitat or by taxonomic category of host (i.e. species), we considered each individual small mammal collected as a patch or community of parasites. Each patch was associated with parasite presence/absence in addition to a variable considered 'parasite free' to account for small mammals free of parasites. Using constrained correspondence analysis (a.k.a. canonical correspondence analysis) (CCA) we investigated the influence of the taxonomic classification of each individual and the habitat the individual was from to understand what serves as the best predictor for the parasites of each individual animal captured. CCA was performed for the habitat while conditioning for species and vice versa. The results of each CCA were analysed using an ANOVA-like permutation test for CCA to assess the significance of constraints. All analyses were performed using the Vegan package on the R statistical platform (version 3.0.1) (R Core Team, 2013) following established methods (Bellier, 2012).

RESULTS

From May to July 2009, 327 small terrestrial mammals were collected in and around KNP (Fig. 1). Small mammal density, species richness (rarefied with standard error) and relative abundance of all 3

host species were calculated for each habitat, although density was not calculated for human settlements (Table 1). Mammals collected represented 23 species and parasites varied in prevalence across habitat and host species (Fig. 1). All parasites examined were found to be harboured by *P. jacksoni* and *L. aquilus*, while *H. stella* harboured all but cryptosporidium.

Linear regression was used to investigate parasite prevalence among the various species (Table 2). We identified a significant positive association between the overall small mammal density of a community and the prevalence of trypanosomes ($R^2 = 0{\cdot}586$, $P = 0{\cdot}047$) and lice ($R^2 = 0{\cdot}781$, $P = 0{\cdot}012$) among *P. jacksoni*. Additionally, there was a positive association among the relative abundance of *H. stella* and the prevalence of trypanosomes ($R^2 = 0{\cdot}708$, $P = 0{\cdot}011$) and mites ($R^2 = 0{\cdot}717$, $P = 0{\cdot}010$). Therefore, the more dominant *H. stella* become in the community of small mammals, the more individual *H. stella* are harbouring trypanosomes and mites. Parasite prevalence among *L. aquilus* was more closelyassociated with small mammal species richness with an association with flea infestation ($R^2 = 0{\cdot}755$, $P = 0{\cdot}016$) and trypanosome ($R^2 = 0{\cdot}759$, $P = 0{\cdot}014$). Relationships between habitat disturbance and parasite prevalence were examined using Spearman's rank-order correlation. There was a negative association between habitat disturbance and trypanosome prevalence among *H. stella* ($r_s = -0{\cdot}880$, $P = 0{\cdot}021$). A Bonferroni correction was not applied to these analyses because of the increased criticism of its validity in ecological cases and the increased risk of a Type II error (Krasnov *et al*. 2008). But we cautiously interpreted our data in consideration of Type I error and the consideration that with Bonferroni correction these results would be considered insignificant despite the biological associations.

Correspondence analysis was performed to consider the parasite communities (presence/absence) harboured by each individual. Using the parasite communities associated with each individual within the populations of *P. jacksoni, L. aquilus* and *H. stella*, we investigated the influence of habitat and/or taxonomic classification on the parasite community. We found that a host's parasite community was more closely associated with other individuals of that same host species than to other hosts within their same habitat but of various species. When the species was controlled and the habitat type was examined, no significant associations were identified ($P = 0{\cdot}784$) (Fig. 2A). Alternatively, when habitat was controlled, the species was significantly clustered ($P < 0{\cdot}0001$) (Fig. 2B).

DISCUSSION

Generalized laws and theories, which are broadly applicable and repeatable under various conditions, were used to understand ecological interactions (Lawton, 1999; Lange, 2005; Poulin, 2007). We investigated a broad range of habitat types that harbour diverse communities of host species as well as parasites. We focused our study on a single point in time and identified relatively a few patterns of parasitism among host species. In general, we did not identify any universal relationships or patterns. Despite the preliminary nature of our study, this work does provide additional empirical evidence for the importance of understanding host taxonomy and parasite specificity (Froeschke *et al*. 2013).

Several patterns among the different species did emerge in this study, although at this point we can only speculate as to the dynamic drivers. Among the *P. jacksoni* population in forested Uganda, we found an association between trypanosomes and lice prevalence and increases in small mammal density. It is accepted that both lice and trypanosomes are moderately host-specific, usually infecting multiple hosts of restricted phylogenies or taxonomic classifications (Dobigny *et al*. 2011; Froeschke *et al*. 2013). Therefore, the association we found between parasite prevalence and total small mammal density (as opposed to relative abundance of *P. jacksoni*) may be associated with spill-over of trypanosomes and lice from other dominant host species. This pattern may also be indicative of a decline in host resistance in competitive environments (Johnson *et al*. 2013). Interestingly, trypanosome prevalence among *H. stella* was associated with increases in relative abundance and habitat disturbance which may indicate *H. stella* as a potential primary native host for trypanosomes in addition to possible spill-over from other invasive host species in the disturbed habitats. One of the most common species of trypanosome-infecting rodents is *Trypanosoma lewisi* which is a globally invasive parasite of rodents and transmitted from invasive *Rattus rattus* into wild populations (Dobigny *et al*. 2011). *Lophuromys aquilus* experienced a positive association of both trypanosomes and fleas and overall small mammal richness, which may compete with hypotheses that predict an increase in host species richness leads to declines in host-specific parasite prevalence. This relationship between trypanosomes and fleas among *L. aquilus* and overall small mammal richness may also be explained by spill-over if these parasites are less host-specific and have the ability to infect a wide range of hosts. Additionally, we found an association between mite prevalence on *H. stella* and relative abundance of *H. stella*, which is not a surprising association since mites are recognized as being predominately host-specific and we would suspect their infestation rate to increase as the available hosts increase (Fain, 1994). We did not find any linear associations among ticks, *Giardia* or *Cryptosporidium*.

Table 1. In total, 327 small mammals representing 23 distinct species were collected from 7 habitats in and around Kibale National Park. Each habitat experienced varied levels of host density, species richness (rarefied) and disturbance level. Each individual small mammal was screened for a variety of parasites – *Giardia* spp., *Cryptosporidium* spp., *Trypanosoma* spp., mites, lice, fleas and ticks. The numbers in each parasite column (*Giardia, Cryptosporidium*, etc.) indicate the number of host from each individual species infected with each parasite group

Species	Species richness (standard error)	Trapping effort	Density/ trap success	Total number collected	Relative abundance (%)	*Trypanosoma*	*Giardia*	*Cryptos-poridium*	Ticks	Mites	Fleas	Lice
Hylomyscus stella				11	41	2	0	0	6	11	0	0
Malacomys longipes				1	4	0	0	0	0	1	0	0
Praomys jacksoni				11	41	1	0	0	4	11	3	0
Praomys misonnei				4	15	1	0	0	0	4	0	2
Total in habitat	4·00 (0·00)	918	0·029	27		4	0	0	10	27	3	2
Hybomys lunaris				1	2	0	0	0	0	1	0	0
Hylomyscus stella				14	21	2	0	0	8	14	4	1
Lophuromys aquilus				1	2	0	0	0	0	1	0	1
Malacomys longipes				2	3	0	0	0	0	2	1	1
Mastomys natalensis				1	2	0	0	0	1	1	1	0
Praomys jacksoni				29	44	11	2	0	8	29	9	11
Praomys misonnei				18	27	1	0	0	4	18	5	6
Total in habitat	4·88 (0·95)	918	0·072	66		14	2	0	21	66	20	20
Hybomys lunaris				3	8	2	0	0	1	3	1	2
Hylomyscus stella				13	34	2	0	0	4	13	5	1
Lophuromys aquilus				3	8	0	3	1	0	1	0	1
Mus bufo				2	5	0	0	0	0	2	1	0
Praomys jacksoni				16	42	7	0	0	5	16	9	11
Praomys misonnei				1	3	0	0	0	0	1	0	1
Total in habitat	5·59 (0·55)	459	0·0828	38		11	3	1	10	36	16	16
Crocidura dolichura				1	3	0	0	0	0	1	0	0
Crocidura fuscomurina				1	3	0	0	0	0	0	0	0
Crocidura nigrofusca				2	5	0	0	0	2	1	2	1
Dasymys incomtus				1	3	0	0	0	0	1	0	0
Hylomyscus stella				1	3	0	0	0	1	1	0	0
Lophuromys aquilus				4	10	0	2	1	3	4	1	3
Mus grata				6	15	0	0	0	2	4	0	0
Praomys jacksoni				23	59	12	1	0	9	21	5	14
Total in habitat	6·67 (0·92)	459	0·085	39		12	3	1	17	33	8	18
Crocidura littoralis				1	2	0	0	0	1	0	1	0
Crocidura maurisca				1	2	0	0	0	1	1	0	0
Crocidura olivieri				1	2	0	0	0	0	1	1	0
Dendromus mystacalis				1	2	0	0	0	0	1	0	0
Gerbilliscus kempi ruwenzorii				5	11	0	0	0	1	5	1	2
Hybomys lunaris				1	2	0	0	0	0	0	0	0
Hylomyscus stella				8	17	0	0	0	2	7	1	0
Lemniscomys striatus				3	6	3	0	0	1	3	2	0
Lophuromys aquilus				5	11	1	2	0	1	5	3	2
Mus grata				6	13	0	1	0	1	6	2	2

Table 1. (*Cont.*)

Species	Species richness (standard error)	Trapping effort	Density/ trap success	Total number collected	Relative abundance (%)	*Trypanosoma*	*Giardia*	*Cryptos-poridium*	Ticks	Mites	Fleas	Lice
Oenomys hypoxanthus				1	2	0	0	0	0	1	0	0
Praomys jacksoni				14	30	1	0	0	2	13	6	3
Total in habitat	9·35 (1·16)	918	0·0512	47		5	3	0	10	43	17	9
Crocidura nigrofusca				1	2	0	0	0	1	0	0	1
Crocidura olivieri				1	2	0	0	0	1	0	1	0
Gerbilliscus kempi ruwenzorii				2	4	0	0	0	2	2	1	1
Lophuromys aquilus				31	62	0	21	3	15	30	6	18
Mus grata				7	14	0	0	0	5	6	1	3
Oenomys hypoxanthus				2	4	0	0	0	2	1	0	2
Praomys jacksoni				4	8	0	0	0	1	4	2	2
Rattus rattus				1	2	0	0	0	0	0	0	0
Scutisorex somereni[1]				1	2	0	0	0	1	0	1	0
Total in habitat	6·71 (1·09)	918	0·0545	50		0	21	3	28	43	12	27
Crocidura olivieri				4	7	0	0	0	0	0	1	3
Hylomyscus stella				1	2	0	0	0	1	1	0	0
Lophuromys aquilus				3	5	0	2	1	2	3	1	3
Mus grata				5	8	0	0	0	3	3	0	0
Mus triton				4	7	3	0	0	2	3	0	3

Table 2. Linear regression was used to investigate relationships between parasite prevalence and small mammal density, species richness and relative species abundance of the 3 most abundant rodent species (*P. jacksoni, L. aquilus* and *H. stella*). Additionally, correlation between habitat disturbance and parasite prevalence among these 3 host species was examined using Spearman's rank-order correlation test. Human settlements were omitted from the analysis of small host density.

	Total small mammal density			Relative species abundance			Species richness			Habitat disturbance		
Parasite	*Praomys jacksoni*	*Lophuromys aquilus*	*Hylomyscus stella*	*Praomys jacksoni*	*Lophuromys aquilus*	*Hylomyscus stella*	*Praomys jacksoni*	*Lophuromys aquilus*	*Hylomyscus stella*	*Praomys jacksoni*	*Lophuromys aquilus*	*Hylomyscus stella*
Trypanosoma spp.	$R^2 = 0{\cdot}586$ $P = 0{\cdot}047$	ns	ns	ns	ns	$R^2 = 0{\cdot}708$ $P = 0{\cdot}011$	ns	$R^2 = 0{\cdot}759$ $P = 0{\cdot}016$	ns	ns	ns	$r_s = -0{\cdot}880$ $P = 0{\cdot}021$
Giardia spp.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cryptosporidium spp.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ticks	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Mites	ns	ns	ns	ns	ns	$R^2 = 0{\cdot}717$ $P = 0{\cdot}010$	na	ns	ns	ns	ns	ns
Fleas	ns	ns	ns	ns	ns	ns	ns	$R^2 = 0{\cdot}755$ $P = 0{\cdot}016$	ns	ns	ns	ns
Lice	$R^2 = 0{\cdot}781$ $P = 0{\cdot}012$	ns	ns	ns	na	na	ns	ns	ns	ns	ns	ns

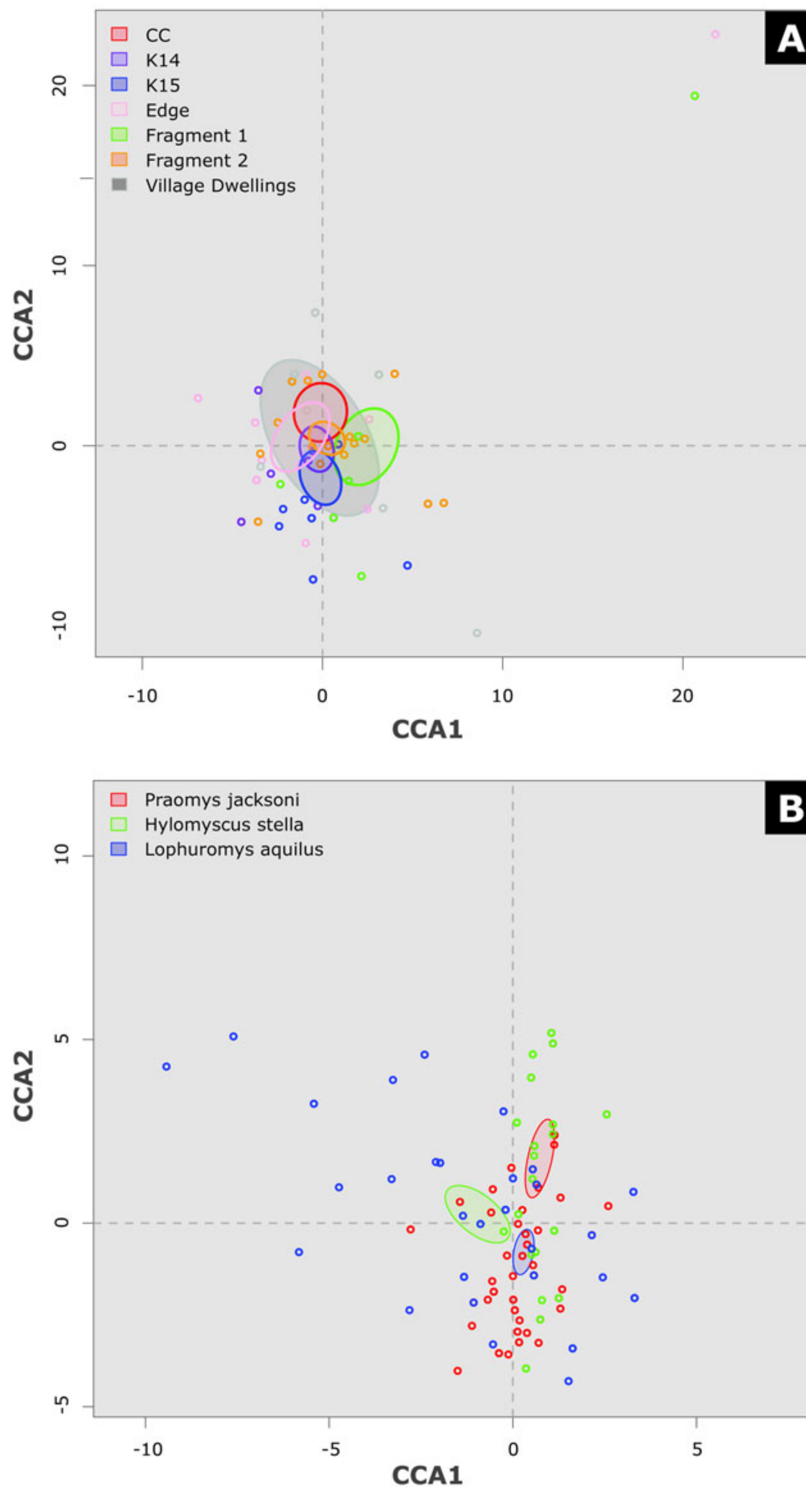

Fig. 2. (A) Correspondence analysis of habitats associated with KNP using parasite communities within each habitat harboured the most abundant rodent species – *P. jacksoni*, *L. aquilus* and *H. stella*. The 7 habitats are shown in the ordination plot represent a gradient of habitat disturbance (least to most disturbed is listed from top to bottom in the figure key) with each habitat represented by a specific colour indicated in the figure key and each point an individual. Some points are superimposed on each other. The correspondence analysis determined parasite communities on each individual small mammal were not associated with the habitat the host occupied. (B) Correspondence analysis of the parasite communities harboured by the 3 most abundant rodent hosts – *P. jacksoni*, *L. aquilus* and *H. stella* sampled from all habitats. Each species is represented by a specific colour indicated in the figure key and each point represents an individual. Ellipses represent 95% confidence interval of the species centroid, and non-overlapping ellipses are interpreted as significant differences between the species at $\alpha = 0{\cdot}05$. Some points are superimposed on each other. All 3 rodent species show distinct parasite community differences. The correspondence analysis determined parasite communities were significantly associated with taxonomic classification of their host species ($P = 0{\cdot}0001$).

Our study highlights the importance of taxonomic classification of host species to understand their parasite communities, with environmental factors being a secondary influence on a host's parasite community. Our results support recent findings that relationships between biodiversity and pathogen transmission are idiosyncratic and highly dependent on the host species and parasites studied (Salkeld *et al*. 2013). It is possible that general patterns between parasite prevalence and host dynamics/environment would emerge in more simplistic community assemblages of small mammals experiencing less extensive habitat disturbance. Additionally, there are possible factors and interactions unaccounted for in our work, which may be more influential on parasite prevalence than those examined in our present study. Such factors in more disturbed habitats could likely include pathogen spill-over from human and domestic animal sources, the influence of invasive species (and their parasites), and alterations in individual host susceptibility to parasites (Daszak *et al*. 2000; Torchin *et al*. 2003; Dobson *et al*. 2008). General linear patterns associated with parasitism among different host communities are likely more easily identified when these communities examined maintain a certain level of shared species and experience a more gradual gradient of habitat disturbance. To more accurately investigate relationships between host diversity and parasite prevalence/richness in KNP, we would need to have a larger sampling effort with substantial replications over multiple sites and seasons. The sampling in this study was from 7 distinct habitats experiencing distinct small mammal communities with an absence of paired samplings. Replicate sites would need to first be identified and then sampled at various time points to more accurately answer questions related to the dilution effect and amplification of parasites in forested Uganda.

The coarseness of the parasite data limits our ability to identify the host species responsible for the maintenance of specific parasites within these communities and parasite–host specificity. Future studies could provide further taxonomic characterizations of these parasites to the species level. This finer examination of parasites, particularly the ectoparasites, would certainly identify even greater parasite richness and identify parasite–host dynamics specific to KNP (Alvarado-Otegui *et al*. 2012; Salyer *et al*. 2012). Despite the coarseness of the data and the innate limitations, host taxonomy is still significant in determining the parasites an individual harbours. Further identification of parasite species will only strengthen this finding. Additionally, given recent identification of viral anti-bodies circulating in small mammals around KNP, future work using serologic assays would broaden our knowledge of disease life history for each individual small mammal (Salzer *et al*. 2013).

Ecosystems are complex with an intricate network of hosts and parasites. General patterns would be expected to be less common as complexity increases in these natural systems. In the absence of a larger sampling effort, this impact of habitat disturbance, host community density and species richness in Western Ugandan small mammal communities appear less influential in determining parasite prevalence and parasite community. Our data provide empirical evidence that within the small mammal communities in Western Uganda, very few patterns emerged to explain these ecological drivers of parasite prevalence. However, we did find strong associations between individual small mammal taxonomy and the community of parasites they harbour. This study provides further evidence that the parasite communities found in the mosaic landscape in Western Uganda are strongly influenced by the taxonomy of the dominant host species and the natural history of the parasites they harbour.

ACKNOWLEDGEMENTS

We thank the Uganda Wildlife Authority, Uganda National Council for Science and Technology, Makerere University Biological Field Station and local authorities for permission to conduct this study. IACUC committees at Emory University (#062-2009) and the CDC (#1768) approved all animal collection and handling protocols. Additionally, animals from human dwellings were collected with permission from local authorities (Local Chairman) and homeowners. Thanks to R. R. Lash for cartographic contributions and C. Akora and I. Mwesige who provided assistance in the field and K. Cross for assistance in the laboratory. We also thank R. Stevens, W. Stanley, J. Mills, A. Peralta, I. Damon and C. Hughes for helpful comments, logistical and/or analytical assistance. The views expressed in this paper are solely those of the authors and do not represent those of the CDC, US Government or any other entity which the authors may be affiliates. Lastly, we are very grateful to two anonymous reviewers for their helpful comments and expertise.

FINANCIAL SUPPORT

This research was supported in part by the Emory Global Health Institute, Emory University Environmental Sciences Department and the appointment of J.S.S. to the Research Participation Programme administered by Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement with CDC.

REFERENCES

Alvarado-Otegui, J. A., Ceballos, L. A., Orozco, M. M., Enriquez, G. F., Cardinal, M. V., Cura, C., Schijman, A. G., Kitron, U. and Gurtler, R. E. (2012). The sylvatic transmission cycle of *Trypanosoma cruzi* in a rural area in the humid Chaco of Argentina. *Acta Tropica* **124**, 79–86.

Anderson, D. R., Burnham, K. P., White, G. C. and Otis, D. L. (1983). Density-estimation of small-mammal populations using a trapping web and distance sampling methods. *Ecology* **64**, 674–680.

Arneberg, P. (2002). Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**, 88–94.

Beldomenico, P. M. and Begon, M. (2010). Disease spread, susceptibility and infection intensity: vicious circles? *Trends in Ecology and Evolution* **25**, 21–27.

Bellier, E. (2012). D. Borcard, F. Gillet, P. Legendre: Numerical Ecology with R. *Journal of Agricultural, Biological, and Environmental Statistics* **17**, 308–309.

Bush, S. E. (2009). *Field Guide to Collecting Parasites*. Natural History Museum, University of Kansas, Lawrence, Kansas, USA.

Bush, S. E., Reed, M. and Maher, S. (2013). Impact of forest size on parasite biodiversity: implications for conservation of hosts and parasites. *Biodiversity and Conservation* **22**, 1391–1404.

Chapman, C. A. and Lambert, J. E. (2000). Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *American Journal of Primatology* **50**, 169–185.

Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P. and Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation Biology* **14**, 207–217.

Daszak, P., Cunningham, A. A. and Hyatt, A. D. (2000). Wildlife ecology – emerging infectious diseases of wildlife - threats to biodiversity and human health. *Science* **287**, 443–449.

Delany, M. J. (1975). *The Rodents of Uganda*, Trustees of the British Museum (Natural History), London, UK.

Dobigny, G., Poirier, P., Hima, K., Cabaret, O., Gauthier, P., Tatard, C., Costa, J. M. and Bretagne, S. (2011). Molecular survey of rodent-borne Trypanosoma in Niger with special emphasis on *T. lewisi* imported by invasive black rats. *Acta Tropica* **117**, 183–188.

Dobson, A. (2004). Population dynamics of pathogens with multiple host species. *American Naturalist* **164**, S64–S78.

Dobson, A., Lafferty, K. D., Kuris, A. M., Hechinger, R. F. and Jetz, W. (2008). Homage to Linnaeus: how many parasites? How many hosts? *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11482–11489.

Dranzoa, C. (1998). The avifauna 23 years after logging in Kibale National park, Uganda. *Biodiversity and Conservation* **7**, 777–797.

Fain, A. (1994). Adaptation, specificity, and host-parasite coevolution in mites (Acari). *International Journal for Parasitology* **24**, 1273–1283.

Froeschke, G., van der Mescht, L., McGeoch, M. and Matthee, S. (2013). Life history strategy influences parasite responses to habitat fragmentation. *International Journal for Parasitology* **43**, 1109–1118.

Gillespie, T. R. and Chapman, C. A. (2006). Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. *Conservation Biology* **20**, 441–448.

Gillespie, T. R. and Chapman, C. A. (2008). Forest fragmentation, the decline of an endangered primate, and changes in host–parasite interactions relative to an unfragmented forest. *American Journal of Primatology* **70**, 222–230.

Gillespie, T. R., Chapman, C. A. and Greiner, E. C. (2005). Effects of logging on gastrointestinal parasite infections and infection risk in African primates. *Journal of Applied Ecology* **42**, 699–707.

Hartter, J. (2009). Attitudes of rural communities toward wetlands and forest fragments around Kibale National Park, Uganda. *Human Dimensions of Wildlife* **14**, 433–447.

Hartter, J., Ryan, S. J., Southworth, J. and Chapman, C. A. (2011). Landscapes as continuous entities: forest disturbance and recovery in the Albertine Rift landscape. *Landscape Ecology* **26**, 877–890.

Isabirye-Basuta, G. and Kasenene, J. M. (1987). Small rodent populations in selectively felled and mature tracts of Kibale Forest, Uganda. *Biotropica* **19**, 260–266.

Johnson, P. T. J., Preston, D. L., Hoverman, J. T. and Richgels, K. L. D. (2013). Biodiversity decreases disease through predictable changes in host community competence. *Nature* **494**, 230–233.

Kasenene, J. M. (1984). The influence of selective logging on rodent populations and the regeneration of selected tree species in the Kibale Forest, Uganda. *Tropical Ecology* 179–195.

Keesing, F., Belden, L. K., Daszak, P., Dobson, A., Harvell, C. D., Holt, R. D., Hudson, P., Jolles, A., Jones, K. E., Mitchell, C. E., Myers, S. S., Bogich, T. and Ostfeld, R. S. (2010). Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* **468**, 647–652.

Krasnov, B. R., Korallo-Vinarskaya, N. P., Vinarski, M. V., Shenbrot, G. I., Mouillot, D. and Poulin, R. (2008). Searching for general patterns in parasite ecology: host identity versus environmental influence on gamasid mite assemblages in small mammals. *Parasitology* **135**, 229–242.

Lafferty, K. D. (2010). Interacting parasites. *Science* **330**, 187–188.

Lafferty, K. D. (2012). Biodiversity loss decreases parasite diversity: theory and patterns. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 2814–2827.

Lane, R. P., Crosskey, R. W. (Ed.) (1993). *Medical Insects and Arachnids*. Kluwer Academic Publishers, Dordrecht, Netherlands.

Lange, M. (2005). Ecological laws: what would they be and why would they matter? *Oikos* **110**, 394–403.

Lawton, J. H. (1999). Are there General Laws in Ecology? *Oikos* **84**, 177–192.

Lwanga, J. (1994). The role of seed and seedling predators, and browsers on the regeneration of two forest canopy species (Mimusops Bagshawei and Strombosia Scheffleri) in Kibale Forest, Reserve, Uganda. Ph.D. thesis, University of Florida, Gainsville.

Mills, J. N., Childs, J. E., Ksiazek, T. G. and Peters, C. J. (1995). *Methods for Trapping and Sampling Small Mammals for Virologic Testing*, US Department of Health and Human Services, Public Health Service, CDC, Atlanta, Georgia.

Mills, J. N., Yates, T. L., Ksiazek, T. G., Peters, C. J. and Childs, J. E. (1999). Long-term studies of hantavirus reservoir populations in the southwestern United States: rationale, potential, and methods. *Emerging Infectious Diseases* **5**, 95–101.

Nagorsen, D. W. and Peterson, R. L. (1980). *Mammal Collector's Manual*. Royal Ontario Museum, Toronto.

Noyes, H. A., Stevens, J. R., Teixeira, M., Phelan, J. and Holz, P. (1999). A nested PCR for the ssrRNA gene detects *Trypanosoma binneyi* in the platypus and *Trypanosoma* sp. in wombats and kangaroos in Australia. *International Journal for Parasitology* **29**, 331–339.

Noyes, H. A., Ambrose, P., Barker, F., Begon, M., Bennet, M., Bown, K. J. and Kemp, S. J. (2002). Host specificity of *Trypanosoma* (Herpetosoma) species: evidence that bank voles (*Clethrionomys glareolus*) carry only one T. (H.) evotomys 18S rRNA genotype but wood mice (*Apodemus sylvaticus*) carry at least two polyphyletic parasites. *Parasitology* **124**, 185–190.

Ostfeld, R. S., Keesing, F. and Eviner, V. T. (2008). *Infectious Disease Ecology: Effects of Ecosystems on Disease and of Disease on Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.

Peppers, L. L., Carroll, D. S. and Bradley, R. D. (2002). Molecular systematics of the genus *Sigmodon* (Rodentia: Muridae): evidence from the mitochondrial cytochrome-b gene. *Journal of Mammalogy* **83**, 396–407.

Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology* **134**, 763–776.

R Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Randolph, S. E. and Dobson, A. D. M. (2012). Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology* **139**, 847–863.

Roche, B., Dobson, A. P., Guegan, J. F. and Rohani, P. (2012). Linking community and disease ecology: the impact of biodiversity on pathogen transmission. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 2807–2813.

Salkeld, D. J., Padgett, K. A. and Jones, J. H. (2013). A meta-analysis suggesting that the relationship between biodiversity and risk of zoonotic pathogen transmission is idiosyncratic. *Ecology Letters* **16**, 679–686.

Salyer, S. J., Gillespie, T. R., Rwego, I. B., Chapman, C. A. and Goldberg, T. L. (2012). Epidemiology and molecular relationships of *Cryptosporidium* spp. in people, primates, and livestock from Western Uganda. *PLoS Neglected Tropical Diseases* **6**, e1597.

Salzer, J. S., Rwego, I. B., Goldberg, T. L., Kuhlenschmidt, M. S. and Gillespie, T. R. (2007). *Giardia* sp and *Cryptosporidium* sp infections in primates in fragmented and undisturbed forest in western Uganda. *Journal of Parasitology* **93**, 439–440.

Salzer, J. S., Carroll, D. S., Rwego, I. B., Li, Y., Falendysz, E. A., Shisler, J. L., Karem, K. L., Damon, I. K. and Gillespie, T. R. (2013). Serologic evidence for circulating Orthopoxviruses in peridomestic rodents from rural Uganda. *Journal of Wildlife Diseases* **49**, 125–131.

Seavy, N. E. and Apodaca, C. K. (2002). Raptor abundance and habitat use in a highly-disturbed-forest landscape in western Uganda. *Journal of Raptor Research* **36**, 51–57.

Struhsaker, T. T. (1997). *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. University of Florida, Gainsville, Florida.

Telfer, S., Lambin, X., Birtles, R., Beldomenico, P., Burthe, S., Paterson, S. and Begon, M. (2010). Species interactions in a parasite community drive infection risk in a wildlife population. *Science* **330**, 243–246.

Thorn, E. and Kerbis Peterhans, J. (2009). *Small Mammals of Uganda*, Booner Zoologische Monographien, Bonn, Germany.

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J. and Kuris, A. M. (2003). Introduced species and their missing parasites. *Nature* **421**, 628–630.

Woolhouse, M. E. J., Dye, C., Etard, J. F., Smith, T., Charlwood, J. D., Garnett, G. P., Hagan, P., Hii, J. L. K., Ndhlovu, P. D., Quinnell, R. J., Watts, C. H., Chandiwana, S. K. and Anderson, R. M. (1997). Heterogeneities in the transmission of infectious agents: implications for the design of control programs. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 338–342.

Young, H., Griffin, R. H., Wood, C. L. and Nunn, C. L. (2013). Does habitat disturbance increase infectious disease risk for primates? *Ecology Letters* **16**, 656–663.