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Author(s): Tara J. Cepon-Robins, Melissa A. Liebert, Theresa E. Gildner, Samuel S. Urlacher, Alese M. Colehour, J. Josh Snodgrass, Felicia C. Madimenos, and Lawrence S. Sugiyama
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SOIL-TRANSMITTED HELMINTH PREVALENCE AND INFECTION INTENSITY AMONG GEOGRAPHICALLY AND ECONOMICALLY DISTINCT SHUAR COMMUNITIES IN THE ECUADORIAN AMAZON

Tara J. Cepon-Robins, Melissa A. Liebert, Theresa E. Gildner, Samuel S. Urlacher*, Alese M. Colehour, J. Josh Snodgrass, Felicia C. Madimenos†, and Lawrence S. Sugiyama

Department of Anthropology, University of Oregon, Eugene, Oregon 97403. Correspondence should be sent to: *tcepon@uoregon.edu*

ABSTRACT: Soil-transmitted helminth (STH) infections can result in a variety of negative health outcomes (e.g., diarrhea, nutritional deficiencies). Market integration (MI; participation in market-based economies) has been suggested to alter levels of STH exposure due to associated changes in diet, sanitation, and behavior, but the effects are complicated and not well understood. Some effects of economic development result in decreased exposure to certain pathogens, and other factors can lead to higher pathogen exposure. With geographic location used as a proxy, the present study investigates the effects of economic development on parasite load among an indigenous population at multiple points along the spectrum of MI. This research has many implications for public health, including an increased understanding of how social and economic changes alter disease risk around the world and how changing parasite load affects other health outcomes (i.e., allergy, autoimmunity). Specifically, this study examines the prevalence of intestinal helminths among the Shuar, an indigenous group in the Morona-Santiago region of Ecuador, from 2 geographically/economically separated areas, with the following objectives: (1) report STH infection prevalence and intensity among Shuar; (2) explore STH infection prevalence and intensity as it relates to age distribution in the Shuar population; (3) compare STH infection patterns in geographically and economically separated Shuar communities at different levels of MI. Kato-Katz thick smears were made from fresh stool samples and examined to determine STH presence/intensity. Results indicate that 65% of the 211 participants were infected with at least 1 STH. Twenty-five percent of the sample had coinfections with at least 2 species of helminth. Infection was more common among juveniles (<15 yr) than adults. Infection prevalence and intensity was highest among more isolated communities with less market access. This study documents preliminary associations between STH infection and exposure to MI, with implications for public health research and interventions.

Soil-transmitted helminths (STHs), like *Trichuris trichiura* (whipworm), *Ascaris lumbricoides* (roundworm), and *Necator americanus* (hookworm), can cause negative health outcomes, including stunting, wasting, diarrhea, organ failure, nutritional deficiencies, mental and developmental retardation, and death (Bethony et al., 2006; Hurtado et al., 2008; Tanner et al., 2009; Blackwell et al., 2010; Ahmed et al., 2011; Dold and Holland, 2011; Francis et al., 2012). In 2000, more than a third of the world's population was estimated to harbor infection by 1 or more helminths (Elliott et al., 2000; Ahmed et al., 2011). Worldwide, STH infections are also estimated to result in 12,000 to 135,000 deaths annually (World Health Organization [WHO], 2002), with an additional loss of about 39 million disability-adjusted life years (DALYs; 1 DALY is used to represent the loss of 1 healthy year of life) (WHO, 2002; Hotez et al., 2006; Coulibaly et al., 2012). To put this in perspective, traffic accidents, HIV/AIDS, and ischaemic heart disease result in the loss of 41.2, 58.5, and 62.6 million DALYs, respectively (WHO, 2008).

Soil-transmitted helminth infections tend to follow an "over-dispersed" pattern in endemic communities, characterized by high worm burdens in a few individuals and light or no infections in the rest of the population. Those with high worm burden tend to be clustered within households or families (Bethony et al., 2006; Dold and Holland, 2011). Infection with 1 type of STH increases the likelihood of infection with others, most commonly between *T. trichiura* and *A. lumbricoides* (Needham et al., 1998). Although age is 1 of the key factors associated with STH exposure, with most infections occurring in school-aged children (Galvani, 2005), many studies also document high levels of infection among adults, amongst whom infection also shows an overdispersed pattern (Needham et al., 1998; de Silva et al., 2003; Blackwell et al., 2011; Dold and Holland, 2011). However, few studies (Fitton, 2000; Godoy and Cardenas, 2000; Tanner et al., 2009) have been conducted that test these patterns among indigenous populations experiencing social and cultural change associated with rapid economic development and market integration (MI; the emergence of and increased dependence on market-based systems of exchange, resulting in increased consumer goods ownership, processed food consumption, and changes to housing structure and materials).

Soil-transmitted helminths are grouped with other parasitic, bacterial, viral, and fungal infections, all closely associated with poverty, as neglected tropical diseases (NTDs). These diseases are known to contribute to the risk of poverty, because of their debilitating, chronic nature, and they occur disproportionately in "hot spots" that are already experiencing adverse conditions within developing countries (Hotez et al., 2008). Together, Latin America and the Caribbean regions make up 1 of these hot spots, with extremely high economic disparities; an estimated 40% of the approximately 556 million people in this region live below the poverty line (Hotez et al., 2008). Within the Latin American and Caribbean region, the Amazon basin is 1 of the most heavily infected regions, with individuals in indigenous communities often simultaneously experiencing coinfection with STHs, river blindness, leishmaniasis, and other NTDs (Hotez et al., 2008).

It remains unclear to what extent this heavy infection amongst Amazonian groups is affected by rapidly changing socioeconomic conditions. Because MI often results in pronounced disparities in socioeconomic status, access to health care, and availability of protective barriers against pathogen exposure (McDade and Nyberg, 2010), it creates a framework for studying how disease burden is affected by economic, dietary, sanitary and health-care–related change. There is some indication that there is a large

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* Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138.
† Department of Anthropology, City University of New York at Queens, New York, New York 11367.
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amount of variation regarding infectious disease exposure and factors related to MI among transitioning populations (Fitton, 2000; Godoy et al., 2005), yet this issue has not been systematically studied with the use of the multidimensional approach offered by MI. Some effects of MI, such as increased consumption of processed food and altered sanitation practices (e.g., boiling water, hand-washing, separate bathroom facilities), are associated with decreased exposure to certain pathogens, and other factors, including increased population density, poor water purification, and animal domestication, are associated with an increase in pathogen exposure and virulence (Strachen, 1989).

Populations experiencing MI often face a double burden associated with increased rates of both infectious and chronic diseases (Barrett et al., 1998). To date, most studies have focused on chronic diseases associated with MI, such as obesity, cardiovascular disease, autoimmune conditions, and type 2 diabetes (Cassel et al., 1960; Dressler, 1985; Bindon, 1995; Bindon et al., 1997; Dressler, 1999; Dressler and Bindon, 2000; Snodgrass et al., 2007; Cepon et al., 2011; Liebert et al., 2013). The effects of MI on infectious disease exposure, specifically STHs, have been largely ignored, even though understanding this relationship is critical for a more complete understanding of the effects of MI on health and more targeted, effective public health interventions.

The present article examines helminth exposure among the Shuar, an indigenous neotropical group of the Ecuadorian Amazon experiencing rapid economic development and social change. Although helminth infection has not been previously studied among the Shuar, 4 lines of evidence suggest that STH infection is a major contributor to negative health. First, previous surveys among nonindigenous Ecuadorian populations show *A. lumbricoides* to be present in between 25% and 45% of the population, whereas hookworm and *T. trichiura* both have a prevalence of 5% to 25% (De Silva et al., 2003). Second, our previous research among the Shuar has shown that 40% of Shuar children are stunted, a much higher prevalence than is found among other indigenous and nonindigenous children living in the same area (Blackwell et al., 2009). Third, our research on immunoglobulin E (IgE; a class of antibody closely associated with parasitic worms) documented overall high IgE levels among Shuar compared to industrialized populations, as well as negative correlations with stature in both children and adults (Blackwell et al., 2010). Finally, we have shown marked variation in MI within and between Shuar communities in association with geographic distance from a centralized market location (Liebert et al., 2013) with relevance to a variety of health conditions, including cardiovascular disease risk (Liebert et al., 2013) and bone density (Madimenos et al., 2011, 2012). The objectives of the present study are threefold:

- Objective One: Report infection prevalence and intensity of STH among the Shuar. We predict that as a group, Shuar will have moderate to high prevalence and intensity of STH infection based on standard definitions (Montresor et al., 1998), because of their local ecology and geographic location within NTD hot spots (Hotez et al., 2008). We also expect to see an overdispersed distribution with a few individuals harboring most of the population's worm burden, because of the proposed nature of STH infection (Needham et al., 1998; Bethony et al., 2006; Dold and Holland, 2011).
- Objective Two: Explore STH infection prevalence and intensity as it relates to age distribution in the Shuar population. We predict that juveniles (<15 yr old) will have higher prevalence and intensity of infections than adults ($\geq$15), based on higher rates of childhood behaviors associated with orofecal contamination and close proximity with other infected children (Nwaneri and Omuemu, 2012).
- Objective Three: Compare STH infection patterns in geographically and economically separated Shuar communities at different levels of MI. We hypothesize that less market-integrated communities—those located deeper within the Amazon rainforest and further from roads allowing market access—will have higher prevalence of STH infection, based on less ability to buffer exposure through housing and sanitation barriers that would confer protection from pathogens (McDade and Nyberg, 2010).

MATERIALS AND METHODS

Study population

The present study was conducted as part of the Shuar Health and Life History Project (SHLHP; www.bonesandbehavior.org/shuar). The Shuar are a large indigenous forager–horticulturalist group (~46,000 individuals in over 668 communities) concentrated in the cross-Cutucú and Upano Valley areas of the Morona-Santiago and Zamora provinces of Ecuador (Fig. 1). Traditionally, horticulture, hunting, and fishing were the foundations of the Shuar economy (Karsten, 1935; Stirling, 1938; Harner, 1984). Now, the accelerating pace of Shuar integration into the regional market economy provides an excellent opportunity to study the health effects associated with social and lifestyle changes. In the isolated region east of the Cutucú mountains (Cross-Cutucú or CC), Shuar continue to follow more traditional lifeways based on hunting, fishing, and horticulture, whereas those in the Upano Valley (UV) are experiencing greater economic change associated with increasing participation in the market economy (Blackwell et al., 2009; Madimenos et al., 2011). Within the UV region, road access and resource depletion has decreased reliance on hunting and fishing, although production of traditional crops such as manioc and plantains continues to provide the dietary staples (Liebert et al., 2013). These staples are supplemented by raising chickens, and purchasing foodstuffs with money earned from selling cows, agricultural goods (e.g., plantains and papayas), and timber, or through wage labor or government jobs.

The present study bases MI measures on geographic location, a key determinant of market access and availability, with UV individuals residing within walking distance of the main road, where trucks allow transport to the town of Sucúa within about 45 min to 1.5 hr. Sucúa is the local market center, with restaurants, stores, and potential access to medical and pharmaceutical care. In contrast, at the time of data collection CC communities in this study could access Sucúa via 1.5–3 hr by motorized canoe (depending on water level) and an additional effective travel time of approximately 5.5–8.5 hr by bus. The CC communities in this study thus have significantly less regular access to markets than UV sample communities, but greater access than most CC communities. Further, CC sample communities in this study have access to a small health center, staffed by a nurse practitioner, where limited medicines and services for minor injuries and illnesses are available. Previous research based on household level data found significant differences in indices of MI between UV and CC communities, with UV Shuar being significantly more market integrated than CC Shuar (Liebert et al., 2013).

Participants and sampling

The present study design was cross-sectional and employed a geographic comparative approach with an age-stratified sample of juveniles (<15 yr) and adults ($\geq$15 yr). Data were collected over 2 field seasons (August–September 2011 and August–September 2012). A total of 211 volunteers ages 0–86 (116 females, 95 males) from 3 communities—1 UV community of ~350 individuals (n = 89; 52 females, 37 males) and 2 CC communities of ~60 and ~300 individuals, respectively (CC1: n = 55, 29 females, 26 males; CC2: n = 67, 35 females, 32 males)—participated in

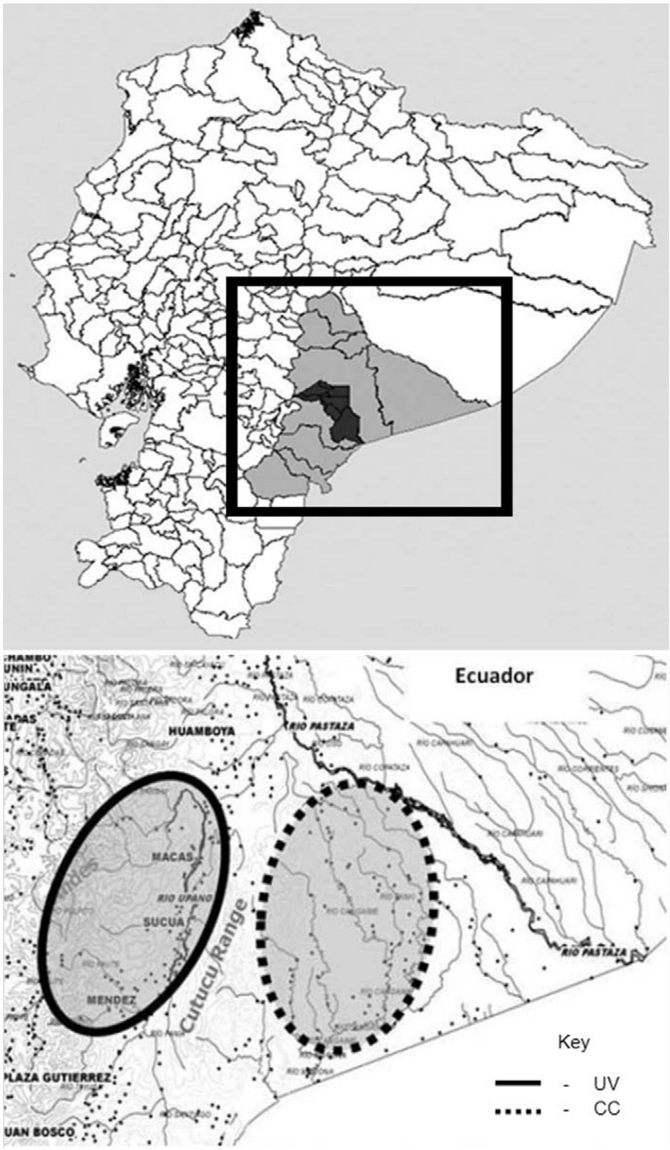

FIGURE 1. Map of Ecuador emphasizing Shuar territory. For this study, Shuar territory is divided into 2 geographically and economically isolated areas: the Upano Valley (UV) and the area across the Cutucu mountain range (CC).

this study. Although conditions in these villages prevented us from obtaining a random sample of residents, we made every effort possible to enroll a sample of participants that was representative of the community in terms of age, socioeconomic status, and style of life (traditional vs. acculturated lifestyles). Participants were recruited on a voluntary basis based on word of mouth and information distributed at community meetings. Although useful for recruiting participants, this method only recruits individuals who are open to health and physiological research, and may overenroll participants concerned about their health.

In this article, we first compare prevalence and intensity of STH infections between CC and UV communities, and then compare each of the sample communities (UV, CC1, and CC2). This was necessary because CC1 was somewhat divergent compared to other CC communities we have worked in previously. CC1 was comprised of a subset of people from a larger community, who recently established CC1 (within the year prior to data collection) when their previous village flooded. It included an extended family that had invested heavily in education, including a very large number of adults who commuted to other communities to work as schoolteachers and earn government wages, putting them in a socioeconomic level above other CC communities. Many in CC1 have close social connections to individuals in the larger towns of Sucúa and Cuenca, and visited and/or worked in these places regularly. Though not as market integrated as UV communities (SHLHP, unpubl. data), CC1 represents a middle ground and demonstrates the complex nature of, and intraregional variation in, the rapidly increasing process of market integration as it spreads throughout the CC region.

Ethics Statement

Informed verbal consent was obtained from adult participants; for participants under 15 (the local age of consent), parental verbal consent and child assent were obtained. Individuals were informed that they could choose not to participate, to participate only in individual portions of the study, or to participate in the full study. The study and consent procedures were approved by the Institutional Review Board (IRB) of the University of Oregon, and the *Federacion de Centros Shuar* (FICSH or Shuar Federation) authorized this research.

Field and laboratory procedures

Stool collection and analysis: Fresh stool samples were collected and processed based on methods established by Raso et al. (2004). A prepacked plastic bag containing an empty stool container marked with the name and identification number of the participant was provided the evening before collection. Participants were instructed to either defecate directly into the cup, or onto a clean, broad leaf or sheet of paper in which case a sample of the feces could be transferred to the container with the use of the clean tongue depressor provided. Participants were asked to only take feces that had not touched another surface (e.g., the ground, dirt, grass). Containers were then returned with a small amount of fresh stool to a centralized village location within an hour of passage, where they were processed within an hour of sample drop off. A single Kato-Katz thick smear (Katz et al., 1972) was prepared from each specimen on a 42-mg plastic template (Vestergaard Frandsen, Lausanne, Switzerland). Kato-Katz thick smears were examined for soil transmitted helminth eggs at ×10 and ×40 microscopy (Cole-Parmer, Vernon Hills, Illinois) in the field by a single trained observer (TJC). Though we looked specifically for evidence of all intestinal parasitic infections that could be found in stool, with the exception of 1 case of tapeworm, only *Ascaris lumbricoides* and *Trichuris trichiura* were present. Helminth egg presence, species presence, species-specific eggs per gram (EPG) of feces, and species-specific infection intensity were recorded. Individuals with greater EPG of feces are infected with a larger number of adult worms and are characterized as having a higher-intensity infection. Infection intensity levels were classified based on EPG cutoffs according to Montresor et al. (1998): *A. lumbricoides* light- (1–4,999 EPG), moderate- (5,000–49,999 EPG) and heavy- ($\geq$50,000 EPG) intensity infection; *T. trichiura* light- (1–999 EPG), moderate- (1,000–9,999 EPG), and heavy- ($\geq$10,000 EPG) intensity infection.

Market integration: For the present study, geographic location was used as a proxy for MI. In addition to ethnographic observation of overall differences in MI between UV and CC communities, previous analyses show that economic and dietary indices of MI differ by study community location as predicted, with UV Shuar being significantly more market integrated than CC Shuar (Liebert et al., 2013; SHLHP, unpubl. data). This comparison was made based on structured interviews used to create variables associated with ownership of goods purchased within a market economy, goods used in traditional subsistence activities, and measures of household construction and access to water/electricity (see Liebert and colleagues [2013] for a more in-depth description of this analysis). Further, these variables associated with MI have been shown, in a preliminary, single-community study to be significantly related to STH infection and intensity (Cepon-Robins et al., unpubl. data).

Age estimation: Ages were determined by birthdates on government identification cards and extensive genealogical information collected by SHLHP, including birth order within families. Overlapping genealogies were collected and cross-checked among multiple informants to ensure accurate age information (Blackwell et al., 2010; Liebert et al., 2013). The split between juvenile (<15) and adult ($\geq$15) was made based on previous research (Blackwell et al., 2010) and local age of consent, or the age at which an individual is considered and treated as an adult within these communities.

TABLE I. Descriptive statistics for all individuals sampled, highlighting significant differences between UV and CC communities. Age and EPG data are presented as mean (SD). Coinfection prevalence is percent based on number of infected individuals.

Descriptive statistics	Full population (n = 211)	UV (n = 89)	CC Combined (n = 126)	CC CC1 (n = 55)	CC CC2 (n = 67)
Age (years)	19.85 (18.38)	19.31 (18.80)	20.23 (18.15)	20.73 (17.62)	19.82 (18.70)
Infection prevalence (%)	64.92	56.18	69.05*	52.7	86.6‖
Coinfection prevalence (%)	25.10	15.70	30.95†	16.30	44.80#
Ascaris lumbricoides prevalence (%)	48.34	28.09	61.11‡	43.60	79.10‖
A. lumbricoides EPG	13,599.06 (19,238.706)	4,418.88 (6572.54)	16,579.64‡ (21,012.28)	11,431.00 (13,596.51)	18,911.09‖ (23,361.295)
Log *A. lumbricoides* EPG	3.58 (0.92)	2.94 (1.02)	3.79‡ (0.79)	3.64 (0.81)	3.85‖ (0.77)
Trichuris trichiura prevalence (%)	38.40	37.10	38.10	25.50	50.70§
T. trichiura EPG	378.07 (623.04)	309.09 (323.10)	425.50 (764.21)	176.57 (163.21)	616.94 (1176.82)
Log *T. trichiura* EPG	2.22 (0.56)	2.26 (0.49)	2.20 (0.62)	2.05 (0.46)	2.27 (0.67)

*,†,‡ Comparisons between UV and CC vary significantly at the 0.05, 0.01, and 0.001 levels, respectively.
§,#,‖ Comparisons between UV, CC1, and CC2 vary significantly at the 0.05, 0.01, and 0.001 levels, respectively.

Statistical analyses

Data analyses were conducted with the use of SPSS version 20.0 (SPSS Inc., Chicago, Illinois). Infection prevalence, *A. lumbricoides* prevalence, and *T. trichiura* prevalence were calculated based on the proportion of participants with any helminth ova, *A. lumbricoides* ova, and *T. trichiura* ova, respectively, in their stool.

The Shapiro-Wilk test was used to test for normality in EPG variables before comparing statistics by age and by community. EPG variables were $\log_{10}$ transformed because of nonnormal distributions. Because of the overdispersed nature of EPG values, extreme outliers were not excluded from the sample because this would have removed data points of particular interest. Both nonparametric tests with nontransformed data and parametric tests with transformed data were used, but results did not significantly differ (Tables I and III); thus parametric tests with transformed variables are reported. Independent-samples *t*-tests were used to compare species specific EPG between coinfected and non-coinfected individuals. Correlations were used to determine relationships between species-specific EPGs in infected individuals.

Sex and age comparisons: Logistic regression was used to determine if age as a continuous variable was a significant predictor of infection status. Pearson chi-square tests were used to compare infection prevalence, coinfection prevalence, and species-specific prevalence between sexes. Independent-samples *t*-tests were used to compare logEPG of *A. lumbricoides* and *T. trichiura* between juveniles (<15 yr) and adults (≥15 yr), and between sexes. Sex was not a significant predictor of any infection variable, so sexes were analyzed together.

Community comparisons: Pearson chi-square tests were used to compare infection prevalence, coinfection prevalence, species prevalence rates, and species-specific infection intensities (light vs. moderate/heavy) between CC and UV. Independent-samples *t*-tests were used to compare age, and logEPG values between UV and CC. Pearson chi-square tests and 1-way ANOVA with post hoc Bonferroni tests were used to compare infection prevalence variables and logEPG values between 3 communities, respectively.

RESULTS

STH prevalence and infection intensity among the Shuar

Table I presents descriptive data on age and STH prevalence/intensity for the sample as a whole and for individual Shuar communities. Overall, 65% of the 211 individuals sampled were infected with at least 1 STH species, and 25.1% of the sample had coinfections with at least 2 STH species. *Ascaris lumbricoides* eggs were present in 48% of all individuals sampled, and *T. trichiura* was present in 38% of individuals sampled. One individual harbored a tapeworm. No evidence of any other intestinal parasites, including hookworm, was found in any of the fecal samples. Based on WHO standards (Montresor et al., 1998), most of the 102 individuals infected with *A. lumbricoides* had moderate-intensity infections (51%), and only 4% had heavy-intensity infections. Similarly, most of the 81 individuals infected with *T.*

TABLE II. Breakdown of STH infection intensity by community using Montresor et al. (1998) standards.

STH type	Sample	Light	Moderate	Heavy
Ascaris lumbricoides	Total (n = 102)	45% (n = 46)	51% (n = 52)	4% (n = 4)
	UV (n = 25)	68% (n = 17)	32% (n = 8)	0% (n = 0)
	Combined CC (n = 77)	38% (n = 29)	57% (n = 44)	5%* (n = 4)
	CC1 (n = 24)	37.5% (n = 9)	62.5% (n = 15)	0%† (n = 0)
	CC2 (n = 53)	37.7% (n = 20)	54.7% (n = 29)	7.6% (n = 4)
Trichuris trichiura	Total (n = 81)	91% (n = 74)	9% (n = 7)	0% (n = 0)
	UV (n = 33)	91% (n = 30)	9% (n = 3)	0% (n = 0)
	Combined CC (n = 48)	92% (n = 44)	8% (n = 4)	0% (n = 0)
	CC1 (n = 14)	100% (n = 14)	0% (n = 0)	0% (n = 0)
	CC2 (n = 34)	88% (n = 30)	12% (n = 4)	0% (n = 0)

* Comparisons of light and moderate/heavy infection intensities between UV and CC vary significantly at the 0.01 level.
† Comparisons of light and moderate/heavy infection intensities between UV, CC1, and CC2 vary significantly at the 0.05 level.

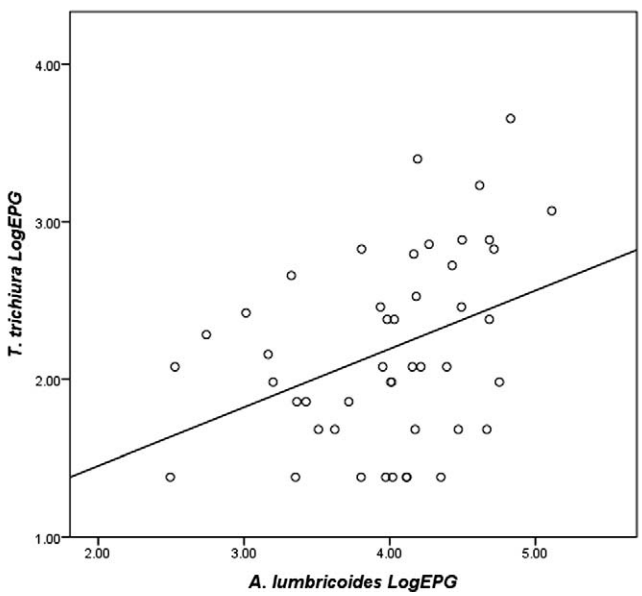

FIGURE 2. Correlation between *Trichuris trichiura* and *Ascaris lumbricoides* infection intensity. Values represent logEPGs for *T. trichiura* and *A. lumbricoides* among infected individuals ($R^2 = 0.143$).

trichiura had light-intensity infections (91%), a few had moderate-intensity infection (9%) and none had heavy infections (Table II).

To understand the extent to which STH infection follows an overdispersed pattern in this sample, we first determined what percent of the worm burden was harbored by individuals with the highest EPG for each species. Of the 102 individuals infected with *A. lumbricoides*, 1 person harbored 9% of all EPGs, and the 5 individuals with the greatest infections harbored 26% of all *A. lumbricoides* EPGs. Similarly, of the 81 individuals infected with *T. trichiura*, the individual with the highest-intensity infection harbored 15% of all *T. trichiura* EPGs, and the 5 individuals with the highest *T. trichiura* EPGs harbored 36% of all *T. trichiura* EPGs. Next, we tested the relationship between species-specific infections among infected individuals. Those individuals with coinfections had higher log *A. lumbricoides* EPG than single-species–infected individuals ($P < 0.001$), though no significant difference was found for *T. trichiura*. Log *A. lumbricoides* and log *T. trichiura* EPG values were significantly positively correlated with each other ($P < 0.001$; Fig. 2).

STH infection and age

Age (as a continuous variable) was not a significant predictor of infection with at least 1 species, coinfection, or *A. lumbricoides* infection. Age was, however, a significant predictor of *T. trichiura* infection ($B = -0.035$, Wald[1] = 12.545, $P < 0.001$). Juveniles were 2.3 times more likely to be infected with at least 1 type of helminth ($B = 0.85$, Wald[1] = 8.32, $P < 0.01$), 4.9 times more likely to be infected with *T. trichiura* ($B = 1.60$, Wald[1] = 24.66, $P < 0.001$), and 2.1 times more likely to harbor coinfections with both *A. lumbricoides* and *T. trichiura* ($B = 0.74$, Wald[1] = 3.67, $P = 0.056$). Age group was not a significant predictor of *A. lumbricoides* infection, though intensity of infection did differ by age group. Both log *A. lumbricoides* EPG ($P < 0.01$) and log *T. trichiura* EPG ($P < 0.01$) differed significantly between groups, with juveniles having significantly higher EPG values in both cases (Table III).

STH infection and market integration

Table I presents STH infection prevalence and intensity data for all Shuar communities combined, as well as separately by region and community. Because all high-intensity *A. lumbricoides* infections were in CC individuals, prevalence of light and combined moderate/heavy infection intensity were compared between communities. When UV and combined CC were compared, the more market-integrated UV region had lower infection prevalence (chi-square[1] = 5.17, $P < 0.05$), coinfection prevalence (chi-square[1] = 9.52, $P < 0.01$), *A. lumbricoides* prevalence (chi-square[1] = 25.28, $P < 0.001$), and *A. lumbricoides* infection intensity (chi-square[1] = 7.015, $P < 0.01$). UV individuals also had significantly lower log *A. lumbricoides* EPG than CC ($P < 0.001$). There was no significant difference in *T. trichiura* prevalence, infection intensity, or log EPG between the 2 groups (Table I).

Next, we compared UV with individual CC communities (CC1 and CC2). Infection prevalence (chi-square[1] = 20.36, $P < 0.001$), coinfection prevalence (chi-square[1] = 12.12, $P < 0.01$), *A. lumbricoides* prevalence (chi-square[1] = 40.50, $P < 0.001$), *A. lumbricoides* infection intensity (chi-square[1] = 7.016, $P < 0.05$), and *T. trichiura* prevalence (chi-square[1] = 8.28, $P < 0.05$) all

TABLE III. Age breakdown for STH prevalence and infection intensity. Coinfection prevalence is percent of infected individuals. EPG values are presented as mean (SD).

Infection variables	Age group	
	0–14 (n = 117)	15+ (n = 94)
Infection prevalence (%)	73.50	54.30*
Coinfection prevalence (%)	30.80	13.80‡
Ascaris lumbricoides prevalence (%)	49.60	46.80
A. lumbricoides EPG	18,264.41 (22,736.17)	7,449.27 (10,773.81)†
Log *A. lumbricoides* EPG	3.84 (0.79)	3.23 (0.97)*
Trichuris trichiura prevalence (%)	53.80	19.10†
T. trichiura EPG	431.24 (667.63)	192.00 (392.38)*
Log *T. trichiura* EPG	2.31 (0.55)	1.91 (0.51)*

*,† Comparisons between UV and CC vary significantly at the 0.01 and 0.001 levels, respectively.
‡ A trend was present for coinfection prevalence ($P = 0.053$).

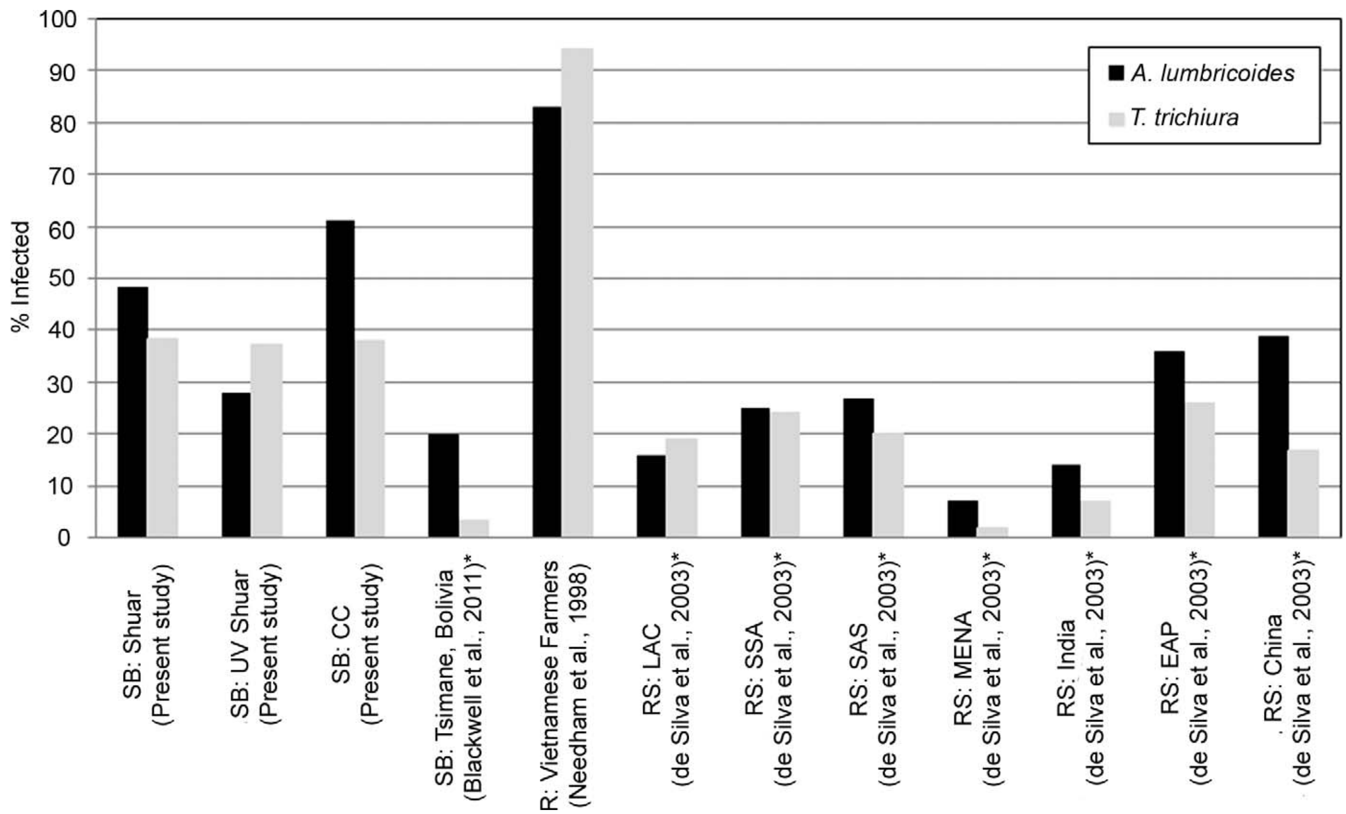

FIGURE 3. *Ascaris lumbricoides* and *Trichuris trichiura* infection by population/region (all age groups). Note: Methods used in some studies (*) differed from the Kato-Katz method used in the present study. Abbreviations: SB, subsistence-based; R, rural; RS, regional survey; LAC, Latin America and the Caribbean; SSA, sub-Saharan Africa; MENA: Middle East and North Africa; SAS, South Asia; EAP, East Asia and the Pacific Islands.

differed significantly between the 3 communities. Log *A. lumbricoides* EPG also differed significantly between the 3 communities ($P < 0.001$). UV had significantly lower log *A. lumbricoides* EPG than both CC1 ($P < 0.05$) and CC2 ($P < 0.001$), but the 2 CC communities did not differ significantly from each other. No difference was found between communities in relation to *T. trichiura* EPG.

When communities were compared individually (Tables I and II), UV had significantly less moderate to heavy intensity *A. lumbricoides* infections than CC1 (chi-square[1] = 4.573, $P < 0.05$). No significant differences were found in infection prevalence, *T. trichiura* prevalence, or coinfection rates between UV and CC1. There was a trend toward significance in *A. lumbricoides* prevalence, with UV having lower infection rates than CC1 (chi-square[1] = 3.660, $P = 0.056$). When UV and CC2 were compared, significantly lower infection rates chi-square[1] = 16.570, $P < 0.001$), *A. lumbricoides* prevalence (chi-square[1] = 39.791, $P < 0.001$), *A. lumbricoides* infection intensity (chi-square[1]= 6.240, $P < 0.05$), and coinfection prevalence (chi-square[1] = 11.589, $P = 0.001$) were present in UV than in CC2. There was no significant difference in *T. trichiura* prevalence between UV and CC2. When the 2 CC communities were compared, CC1 had significantly lower infection prevalence (chi-square[1] = 16.907, $P < 0.001$), *A. lumbricoides* prevalence (chi-square[1] = 16.322, $P < 0.001$), and *T. trichiura* prevalence (chi-square[1] = 8.096, $P = 0.004$) than CC2. Further, there was a trend toward significance when coinfection rates were compared between CC1 and CC2, with CC1 having marginally lower coinfection prevalence (chi-square[1] = 3.346, $P = 0.067$).

DISCUSSION

Figures 3 and 4 present comparative data between this study and other studies of indigenous subsistence-based (SB) populations (San Sebastián and Santi, 2000; Scolari et al., 2000; Tanner et al., 2009; Blackwell et al., 2011), rural (R) populations (Needham et al., 1998; Saldiva et al., 1999; Sackey et al., 2003; Francis et al., 2012), urban (U) populations (Scolari et al., 2000; Francis et al., 2012; Nwaneri and Omuemu, 2012), and regional surveys (RS; De Silva et al., 2003). When compared to previous studies conducted among all age groups, the present study shows much higher rates of infection with both *A. lumbricoides* and *T. trichiura* than most other populations, with the exception of a Vietnamese farming population (Needham et al., 1998; Fig. 3). The Vietnamese population lives in an STH hot spot, with livelihoods dependent on interaction with soil (Needham et al., 1998), increasing their likelihood of infection.

In a comparative study, De Silva et al. (2003) used data from a number of regions to show the global distribution of STHs. Latin America is home to many of the world's NTDs and many individuals suffer related morbidity (Hotez et al., 2008), yet De Silva's estimations for the Latin American/Caribbean (LAC) region is relatively low and fails to capture the high infection rates

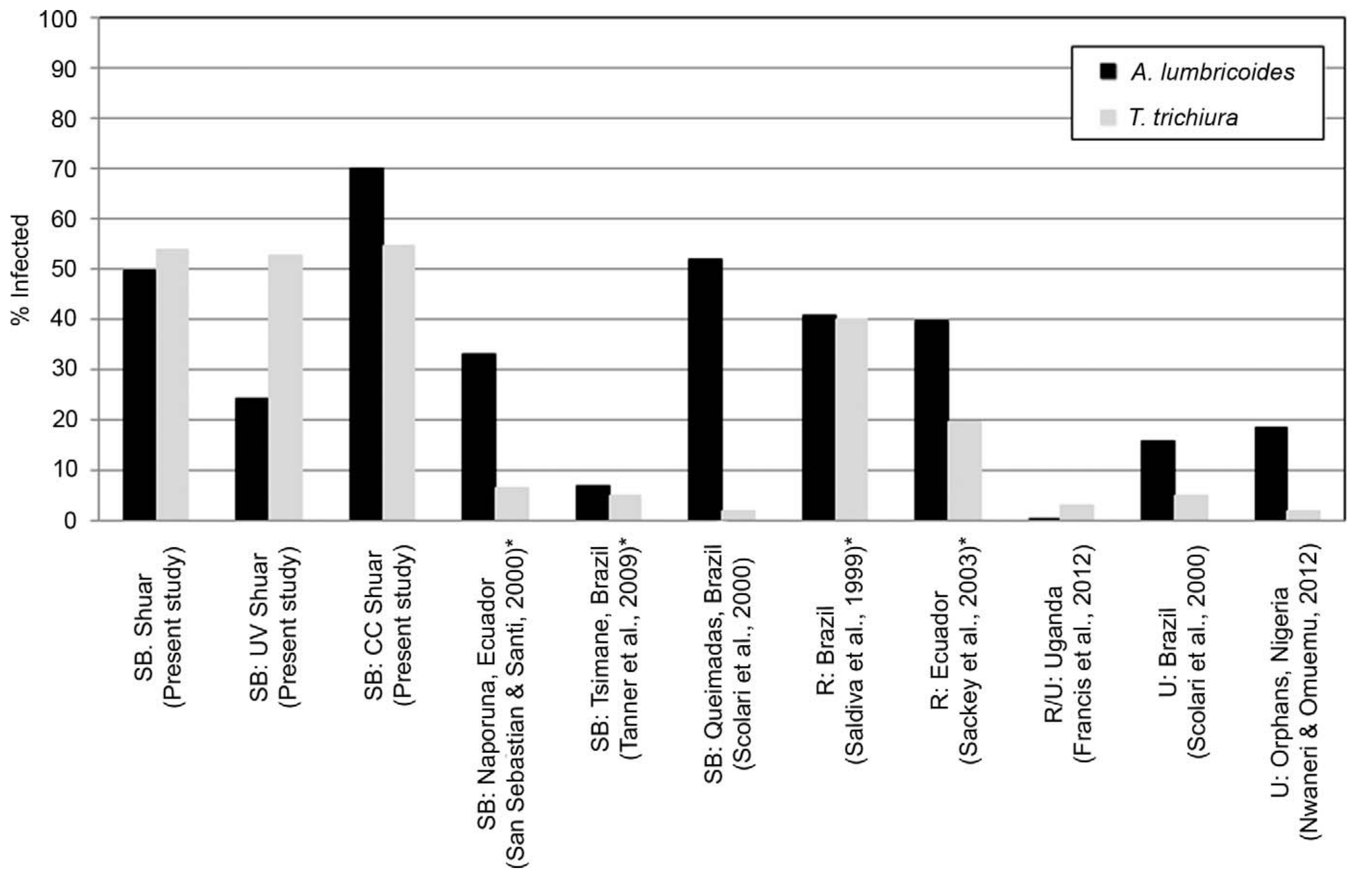

FIGURE 4. *Ascaris lumbricoides* and *Trichuris trichiura* infection by population/region (children only). Note: Methods used in some studies (*) differed from the Kato-Katz method used in the present study. Abbreviations: SB, subsistence-based; R, rural; U, urban.

and intensities experienced by a sampling of its residents in the Amazon (present study).

Compared to infection rates of children from other populations, the present study demonstrated that Shuar children had very high infection rates, particularly children from the CC region (Fig. 4). Interestingly, UV children had similar *A. lumbricoides* infection rates to the other studies and, as a group, a smaller percent of Shuar children were infected with *A. lumbricoides* than subsistence-based Queimadas Children of Brazil (Scolari et al., 2000). Only when CC children are observed alone did this study find comparatively high infection rates. This is not true for *T. trichiura* infection rates. UV, CC, and the combined sample had the highest prevalence of *T. trichiura* of all studies included in this review.

Based on WHO standards (Montresor et al., 1998), the present study found light- to moderate-intensity infections among Shuar for *T. trichiura* and *A. lumbricoides*, respectively. As predicted, we found an overdispersed infection distribution, with a few individuals harboring the majority of eggs. This overdispersed distribution pattern is further demonstrated by the positive correlation between log *A. lumbricoides* EPG and log *T. trichiura* EPG, suggesting that individuals with high EPG of 1 species were more likely to be more heavily infected with the other species. Interestingly, *T. trichiura* infection seemed to be largely associated with age, whereas *A. lumbricoides* infection was associated with community. The fact that they were so closely correlated has interesting implications for research on how and when different helminth species infect human hosts.

Interestingly, no evidence of hookworm infection was documented, even though it is fairly common in other populations around the globe and in Latin America. In comparison, hookworm prevalence among the Tsimane of Bolivia is 45.4% (Blackwell et al., 2011). Of the STHs, hookworm is most closely associated with anemia (Stoltzfus et al., 1997; Tatala et al., 1998; Tsuyuoka et al., 1999; Ezeamama et al., 2008). The absence of evidence for hookworm infection here is consistent with our findings that Shuar hemoglobin levels are primarily in the normal range, with relatively low rates of anemia compared to other South American populations that have been studied (SHLHP, unpubl. data). It is important to note, however, that the absence of hookworm could in part be related to issues with the Kato-Katz method. Although this method is considered the most useful and recommended method available for field studies (WHO, 1991), concerns about its ability to detect hookworm eggs have been raised (WHO, 1991; Tarafder et al., 2010). The Kato-Katz method has been shown to be less sensitive to hookworm infection due to the rapid degeneration of delicate hookworm eggs (Tarafder et al., 2010). Although it is possible that the degeneration of hookworm eggs contributed to the lack of hookworm in the sample, it is unlikely that we would see no evidence of hookworm eggs in any of the sampled individuals if the infection were present. This, combined with hemoglobin data, supports the idea that very little or no hookworm is present in this sample and these communities.

The present study found significant regional differences in the prevalence and intensity of STH infections. Individuals from our CC sample were more likely to be infected with STHs than individuals in the UV sample. Analyzing infection prevalence within the population and then breaking it down in to smaller communities showed the importance of more small-scale studies to capture intracultural and interregional variation within Ecuador and around the world. Simply reporting Ecuadorian data, Amazonian Ecuador data, or even Shuar data fails to capture the experiences of individual communities and can result in suboptimal targeting of public health resources.

Though we found significant differences in infection prevalence between UV and CC communities, UV and CC1 had only minor differences in *A. lumbricoides* prevalence ($P = 0.056$). The only significant differences between the 2 groups were in *A. lumbricoides* EPG ($P < 0.05$) and *A. lumbricoides* infection intensity ($P < 0.05$). Most of the differences between the 3 communities were a result of high infection percentage and elevated EPG values in CC2. As previously discussed, CC1 is an unusual CC community: newly established, relatively small, with a high proportion of residents having government wages as schoolteachers, as well as more intensive ties to the larger towns in the UV. CC1 and CC2 are in short walking distance from each other and use the same river as a water source, suggesting that more than geographic and ecological variability is at play and pointing toward a role for MI in creating variation in parasite exposure.

Further, the similarities in infection prevalence between UV and CC1 suggest a relationship between infection and lifestyle factors associated with overall level of adult education, the good wages associated with teaching school, and their implications for access to markets and medical care, all factors associated with increased MI. CC1 may represent a middle ground between UV and CC2 on the spectrum of MI, facing decreased exposure to STHs based on an increased reliance on market goods/processed foods, sanitary and architectural protective barriers, and less interaction with soil during subsistence-based activities (Strachen, 1989). Increased population density supported by market economies and reliance on horticulture and ownership of domesticated animals, however, may increase the spread of pathogens from person to person if proper sanitary measures are not taken (Barrett et al., 1998). All of these factors, combined with changes in house construction, diet, water source, income, and education level create a complicated picture of MI in transitioning populations (Godoy and Cardenas, 2000).

If the community-level differences in parasite load documented in the present study are related to differences in MI, this research has major implications for understanding recent changes in public health, specifically the rise of allergies and autoimmune disorders. Multiple studies now link the increase in several allergies and autoimmune disorders in developed nations with the concomitant decrease in early life exposure to parasites (Elliott et al., 1999; Nagayama et al., 2004; Fleming and Cook, 2006; Butcher, 2008; Hurtado et al., 2008). The present study suggests a suite of lifestyle-based factors (i.e., MI) contributing to this decrease in parasite exposure and opens doors for public health researchers to understand the social, cultural, and economic changes that may ultimately result in many negative health outcomes associated with MI.

This study has several important limitations. First, the sample size was relatively small and participants were volunteers, which limits the generalization of our findings, by biasing our data toward individuals who were more interested in or concerned about their health. Second, this study uses regional disparities as a proxy for MI. This approach does not allow us to identify specific factors associated with MI that are related to STH infection, and conclusions about MI and parasite load are preliminary. In the future, methods used by Liebert and colleagues (2013) to measure MI based on style of life variables will be used to explore relationships between specific lifestyle factors associated with MI and parasite load among these regionally separated communities.,

Third, very little data are available on access to antihelminth treatments, making it impossible to consider if health-care availability is a driving force in the differences in STH infection rates between UV and CC communities. Both communities report periodic access to antihelminth medications, especially among school-aged children, but school attendance, documentation of treatment, and self-report of treatment are all inconsistent and sporadic. According to the WHO's Preventative Chemotherapy and Transmission Control Database (2012), the last large-scale chemotherapeutic intervention in Ecuador occurred in 2009, when a reported 100% of school-aged children were treated with 2 rounds of albendazole and mebendazole. It is not clear if those treated include indigenous and rural populations, especially those sampled in this study. The lack of large-scale intervention among young children and adults, as well as repeated treatment for school-aged children, results in rapid re-exposure. There is evidence that individuals with predispositions for heavy infection tend to return to pre-treatment levels relatively soon after treatment (Dold and Holland, 2011), suggesting that the differences we see between UV and CC, especially in moderate to heavy infection, would be similar regardless of access to health care, provided medication was not taken immediately prior to sample collection, though more studies are needed to clarify this important issue.

To summarize, the present article found moderate-intensity STH infections that followed an overdispersed pattern among the Shuar, with age predicting infection for all variables except *A. lumbricoides* infection and intensity. Importantly, we found significant differences in rates and intensities of STH infection when geographic distribution was used as a proxy for MI. Participants from the more remote CC communities had higher STH infection prevalence and infection intensities than more market-reliant UV communities, suggesting that MI decreases risk of parasite exposure and/or increases access to treatment. This has important implications for understanding health changes associated with MI. In conjunction with decreased STH infection, we are seeing a heightened risk of chronic diseases among the Shuar with increasing MI (Liebert et al., 2013). Clearly, the relationship between MI and disease risk is complicated, resulting in both negative and positive health outcomes. Although preliminary, this article represents an important step in understanding how parasite exposure is altered by MI and how this alteration may affect overall health.

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