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POPULATION STRUCTURE AND *BARTONELLA QUINTANA* IN HEAD AND BODY LICE IN POKHARA, NEPAL (ANOPLURA: PEDICULIDAE)

Shreekanta S. Poudel and Jefferson A. Vaughan

Biology Department, University of North Dakota, Grand Forks, North Dakota 58202.

Correspondence should be sent to Jefferson A. Vaughan (https://orcid.org/0000-0002-7067-0654) at: *jefferson.vaughan@und.edu*

KEY WORDS

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Head lice
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Pediculosis
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ABSTRACT

This study examined the population structure of head and body lice infesting a random sample of people in Pokhara, Nepal during 2003, 2004, and 2005. A total of 106 participants (6 to 72 yr old, median = 12) volunteered to have lice collected from their heads and clothing. Most participants (70%) harbored only head lice, some (15%) had only body lice, and some (15%) had concurrent infestations of head and body lice (dual infestations). A total of 1,472 lice was collected. Significantly more nymphs were collected than adult lice. Louse populations were generally small (geometric mean = 8.8 lice per person) but a few participants harbored larger louse populations (maximum = 65 lice). People with dual infestations harbored significantly more lice than people with single infestations; however, there was no difference in the infestation intensities between people infested with head lice only vs. those infested with body lice only. Male participants harbored significantly more lice than did females. There were no significant differences in infestation intensity due to participant age or their socioeconomic level. The sex ratio of adult lice was increasingly female biased with increasing adult louse density. Infection of lice with *Bartonella quintana* was low (ca. 1.5%). Pediculosis is a common problem in urban Nepal.

Humans are parasitized by 3 types of lice, each inhabiting distinct regions of the human body. Pubic lice (*Pthirus pubis* L.) live mostly in the pubic hair of adult humans, are typically sexually transmitted, and primarily parasitize sexually active adults. Head lice and body lice are morphologically almost indistinguishable and considered by most authors as a single species, *Pediculus humanus* L., which has evolved into separate ecotypes or subspecies. Body lice are designated by most authors as *P. humanus humanus* L. and head lice are designated as *P. humanus capitis* De Geer. As their common names suggest, head lice live among the hairs of the head and are most commonly found infesting children of all socioeconomic classes. Body lice live in clothing close to the skin of the host and flourish in social settings where people live in close quarters and clothes are not frequently changed (e.g., homeless shelters, refugee camps, etc.). These lice also exhibit other behavioral, physiological, and reproductive differences that promote their reproductive isolation (Veracx and Raoult, 2012). Currently, there are 6 recognized clades of *P. humanus* (i.e., clades A–F) on the basis of the deoxyribonucleic acid (DNA) sequences of 3 mitochondrial gene fragments (Boutellis et al., 2014; Amanzougaghene et al., 2019). All body lice examined to date belong to either clades A or D. Head lice encompass all 6 clades. Clades have their particular geographic distributions. Clade A is the most common and is globally distributed; clade B is found in the Americas, Europe, Australia, Algeria, and Saudi Arabia; clade C is found in some African and Asian countries (including Nepal); clade D is restricted to Africa; clade E is restricted to west Africa, and clade F is restricted to parts of Mexico, Argentina, and Amazonia. *Pediculus humanus* has a long coevolutionary history with humans (Reed et al., 2004) and the geographic distributions of clades have been useful in the reconstruction of prehistoric human migration patterns (Reed et al., 2004; Light et al., 2008; Ascunce et al., 2013; Boutellis et al., 2014; Ashfaq et al., 2015; Amanzougaghene et al., 2016).

The prevalence of human infestation by lice has been most extensively studied with head lice infestations of children. A review of 55 surveys (Falagas et al., 2008) indicated a wide range in prevalence for head lice infestation, varying from 1% to 61%. Although the prevalence of head louse infestations can be high, intensity is usually low. Numerous studies have shown that most infestations are comprised of 10 or fewer lice, including studies in Sri Lanka (65% of 125 heads [Buxton, 1941]), Israel (78% of 342 heads [Mumcuoglu et al., 1990]), Palestine (67% of 340 heads [Al-Shawa, 2006]), and Argentina (88% of 350 heads [Toloza et al., 2009]). A survey in urban Nepal reported a high prevalence of louse infestation in the cities of Pokhara and Kathmandu, with up to 59% of homeless street children having concurrent infestations of head and body lice (Poudel and Barker, 2004), but infestation intensities were not quantified. This report describes the density, age structure, and sex ratio of head and body lice on louse-infested people in Pokhara, Nepal.

MATERIALS AND METHODS

A cross-sectional survey of head and body lice was conducted in Pokhara, Nepal from 2003 to 2005 at 3 different locations within the city—i.e., the Child Worker Concern Center (65 people; ages 6 to 20 yr, median = 11), the Bishram Contact Center (19 people; ages 10 to 72 yr, median = 13), and the local garbage dump (22 people; ages 6 to 40 yr, median = 12). Volunteers were grouped into 3 categories with respect to their living conditions. "Street children" (n = 69) were orphaned or abandoned children who lived without parental care and slept together in groups within rudimentary shelters at recycling yards. "Slum families" were mostly children (n = 28) and a few adults (n = 5) who belonged to economically deprived families living under poor hygienic conditions in small huts near the banks of the Seti River. "Household people" (n = 4) were families living in a more hygienic, middle-class neighborhood. Informed consent was obtained from each participant before examinations were performed. Participants were asked if they had lice and if so, would participants grant permission for workers to collect the lice. For head lice, the participant's hair was examined by combing through the hair for a minimum of 2 min with a commercial nit comb. A small amount of hair conditioner was applied to the scalp, which facilitated combing and helped detect and capture the lice. For body lice, participants removed their shirts and jumpers in privacy and examined their clothes for a minimum of 2 min for body lice. For each participant, the head lice and body lice were placed in separate vials containing ethanol. To maintain confidentiality, samples were coded in such a manner that no identifiers could be used to link a particular sample to a particular participant. Lice in each vial were counted and age graded as either nymphs or adults. Adult lice were sorted by sex, as determined microscopically by the morphologic characteristics of the end of the abdomen and the well-developed genital apparatus visible in the venter of the male abdomen.

All 199 lice collected from 42 people during the 2005 collection were individually homogenized with stainless beads in a TissueLyser II (Qiagen, Germantown, Maryland) and DNA was extracted using guanidine thiocyanate (Tkach and Pawlowski, 1999). The DNA was purified with One-Step PCR Inhibitor Removal kits (Zymogen Research, Irvine, California) and samples were screened individually for *Bartonella* DNA by polymerase chain reaction (PCR) using previously published primers and methodologies (Sasaki et al., 2002, 2006). Positive samples were sequenced using an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Foster City, California). Sequences were trimmed using BioEdit software and compared with sequences in the National Center for Biotechnology Information database.

Infestation rates of head vs. body lice were compared with chi-square or Fisher exact tests. Data for infestation intensity (i.e., number of lice per person) were not randomly distributed (Shapiro–Wilk test, $W = 0.8$, $P < 0.001$). Therefore, count data were transformed by adding 1 to each count and then transforming to logarithms—i.e., $\log10(x + 1)$—before analyses (*t*-tests, analysis of variance, and linear regression). Because count data were skewed and calculations included zero counts, the Williams mean (WM, rather than the arithmetic mean or geometric mean) was chosen to represent the most appropriate measure of central tendency (Alexander, 2012). Six categorical variables were tested to determine if they significantly affected the infestation intensity—i.e., louse type (i.e., head vs. body), participant age, volunteer sex, year of collection, location of collection, and socioeconomic status of the participant. A 0.05 level of significance was used throughout. Data analyses were conducted using Microsoft Excel 2010 (Redmond, Washington) and Statistix 9 (Analytical Software, Tallahassee, Florida).

RESULTS

This study examined the densities of head and body lice infesting 106 people in Pokhara, Nepal who were identified as having pediculosis. They ranged in age from 6 to 72 yr, although most were between 9 and 14 yr of age (median = 12 yr). Most (84%) of the participants were male; a minority (16%) was female. Seventy-four of the 106 participants (70%) harbored only head lice, 16 (15%) harbored only body lice, and 16 (15%) harbored both head and body lice (dual infestations). The prevalence of head louse infestations (85%) significantly exceeded that of body louse infestations (30%) ($\chi^2 = 65.0$, $P < 0.0001$).

Infestation intensity and age structure

A total of 1,472 lice was collected: 1,251 (83%) head lice and 250 (17%) body lice. Infestation intensities ranged from 1 to 62 lice per person, but lice were not randomly distributed among participants (Shapiro–Wilk test, $W = 0.83$, $P < 0.0001$). The WM infestation was 8.8 lice per person (Table I). Infestation intensity varied by year. Participants had significantly greater louse burdens in 2003 (WM = 17.3) than did participants in 2004 (WM = 7.1) and 2005 (WM = 7.0) (Table I). Significantly more nymphal lice per person (WM = 6.2) were collected than adult lice per person (WM = 2.4; $t = -4.7$, df = 205, $P < 0.001$). The mean nymph-to-female ratio was 3.14. Participants with dual infestations harbored significantly more lice (WM = 21.1) than did participants with single infestations (WM = 7.5). There was no difference in infestation intensity between participants with head lice only (WM = 7.6) vs. participants with body lice only (WM = 7.5) ($t = -0.02$, df = 88, $P = 0.984$).

Host demographics

All participants harbored lice. However, male participants harbored significantly more lice (WM = 9.9, n = 88) than did female participants (WM = 5.4, n = 17) ($t = -2.14$, df = 104, $P = 0.035$). There was no effect of a participant's age on the intensity of louse burden ($F = 1.11$, df = 104, $P = 0.352$). Infestation intensity varied by location throughout the city. Participants at the Child Worker Concern Center harbored significantly more lice (WM = 10.5, n = 65) than did participants sampled at the Bishram Contact Center (WM = 5.5; n = 19), but the louse burdens of participants sampled at the dump (WM = 7.8; n = 22) were intermediate and did not

Table I. William mean density (number of people examined) of head lice and body lice among 106 louse-infested people in Pokhara, Nepal, 2003–2005.

Infestation type	2003	2004	2005	All years
Head lice only	21.8 (11)	6.5 (32)	6.0 (31)	7.5 (74)
Body lice only	10. 3 (11)	1.0 (1)	5.2 (4)	7.5 (16)
Dual infestations	38.2 (4)	17.7 (5)	17.8 (7)	21.1 (16)
All lice	17.3 (26)	7.1 (38)	7.0 (42)	8.8 (106)

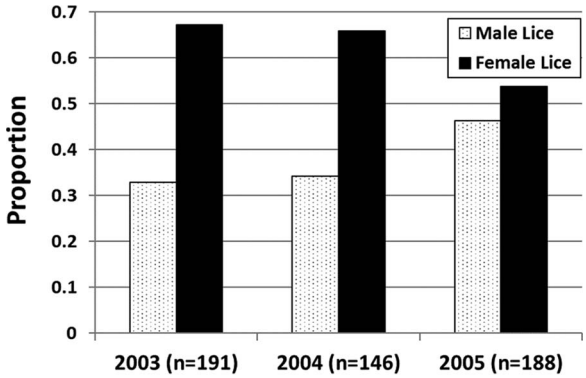

Figure 1. Sex ratios of adult head and body lice collected from infested people in Pokhara, Nepal, 2003–2005.

differ significantly from the other 2 locations ($F = 3.19$, df = 105, $P = 0.045$, Tukey pairwise comparison test). There was no significant effect on the overall louse burden of infested participants with regard to their living conditions ($F = 1.60$, df = 105, $P = 0.192$).

Sex ratios of adult lice

Ninety-seven (91.5%) of 106 participants harbored adult lice. The sex ratios for adult louse populations were generally female biased (Fig. 1). For head and body louse populations combined and for head lice only, the proportions of females were significantly higher than for males (chi-square tests, $P < 0.0001$, $P = 0.006$, respectively). Although a trend in female bias was evident for body lice, the difference was not significant ($P = 0.27$) because of lower sample sizes of adult body lice collected. There was a linear, albeit not very strong ($r^2 = 0.21$), relationship between the densities of female and male lice among individual participants (Fig. 2). Seventeen participants harbored only female lice (11 harbored a single adult female) and 20 participants harbored only male lice (11 harbored a single adult male). Sixty participants harbored both female and male adult lice at densities ranging from 2 to 34 adult lice (Fig. 2). The slope of the relationship between female-to-male lice ($b = 0.54$) was significantly less than 1.0 ($t = -4.24$, df = 95, $P < 0.0001$). This suggests that as adult louse densities increased, sex ratios became progressively more female biased.

Bartonella quintana infection prevalence

Three of 199 lice collected in 2005 tested (1.5%) were PCR positive for *Bartonella quintana* DNA: 1 adult body louse, 1 nymphal head louse, and 1 adult head louse (Table II). Sequencing of the PCR product (partial *16S* ribosomal ribonucleic acid gene) from the adult head louse yielded a 99% sequence identity with the Toulouse strain of *B. quintana*.

DISCUSSION

Surveys of human pediculosis have focused primarily on determining the prevalence of infestation (Falagas et al., 2008). Fewer studies have examined the population structure of human louse infestations. This study examined the population structure of head and body lice collected from 106 people at 3 similar locations in Pokhara, Nepal in 2003, 2004, and 2005. Although the lice collected during this study were not genotyped, a previous survey of lice collected from Pokhara, Nepal during the same time frame (Xiong et al., 2014) reported that 100% of 21 body lice and 91% of 23 head lice examined belonged to clade A. Only a very small proportion (9%) of the head lice collected belonged to clade C. Thus, it is reasonable to assume that most of the lice in this survey probably belonged to clade A. Most infestations were comprised of only head lice (70%), some infestations involved only body lice (15%), and some were comprised of both head and body lice (15%). Overall, the population densities of lice were generally low (ca. 10 lice per person), nymphs outnumbered adults, and females were more numerous than males.

Understanding the typical population structure of human louse infestations is important because population structure may influence the population genetics of lice, which in turn may provide inferences about the effective transmissibility of lice from 1 person to the next, as well as the spread of insecticide resistance. In this regard, it is convenient to think of the totality of lice infesting a single person as an "infrapopulation" and the totality of lice infesting a human population within a specific area (e.g., Pokhara, Nepal) as a "suprapopulation" (Esch et al., 1975). In theory, low effective population sizes or skewed sex ratios in parasite infrapopulations (as observed in this study) may result in genetic homogeneity within an infrapopulation (Loker and Hofkin, 2015). Furthermore, if a parasite exhibits high host specificity and limited host-to-host transmissibility, then there is a strong likelihood that infrapopulations may become genetically differentiated from one another and the entire population (i.e., the suprapopulation) will exhibit a high degree of genetic structure (Huyse et al., 2005).

Genetic structuring among louse infrapopulations has been well documented for chewing lice on pocket gophers and birds (Nadler et al., 1990; Johnson et al., 2002; Nessner et al., 2014; Harper et al., 2015) but has been less studied for lice on humans. In a study of head and body lice, Leo et al. (2005) used 5 microsatellite DNA markers to examine the population genetics of dual infestations of 7 Nepalese street children and 2 sisters from China. That study showed that (1) head and body lice on

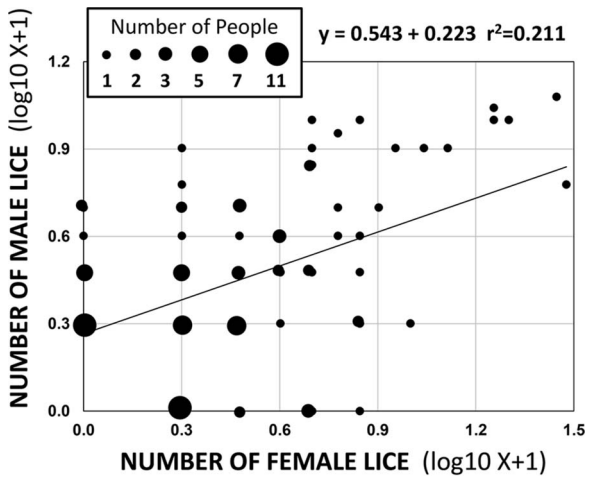

Figure 2. Distribution of adult female and male louse densities ($\log_{10}$ scale) per person. The area of dots corresponds to the number of participants found to harbor a specific density and sex of adult lice, with the smallest dots corresponding to a single person and the largest dots corresponding to 11 people.

Table II. *Pediculus humanus* population structure on 3 people (of 43 examined) who were found to harbor lice positive for *Bartonella quintana* DNA, Pokhara, Nepal, 2005.

Host	Type of infestation	Total lice	No. nymphs	No. adult females	No. adult males	*Bartonella quintana* DNA-positive lice
Male (13 yr)	Body lice only	15	9	1	5	1 adult male louse
Male (8 yr)	Head lice only	14	13	0	1	1 nymphal louse
Male (20 yr)	Head lice only	5	2	1	2	1 adult female louse

individual children were reproductively isolated and genetically distinct from one another and (2) each infested child harbored infrapopulations of head and body lice that were genetically distinct from the infrapopulations infesting the other children, even though the living conditions were such that 5 of the Nepalese children all slept in the same bed. Probability analysis of microsatellite results indicated that some of those louse populations had a high degree of homozygosity and were not in Hardy–Weinberg equilibrium. The dearth of heterozygotes in louse populations may have resulted from a founder effect (i.e., infestation initiated by just a few lice), followed by several generations of inbreeding.

The low density of louse populations found in this survey and in others (Buxton, 1941; Mumcuoglu et al., 1990; Al-Shawa, 2006; Toloza et al., 2009) supports the notion that many louse infestations probably arise from a small number of foundlings. In our survey, louse burdens were generally less than 10 lice per person and comprised mainly of nymphs. Furthermore, only 60 of the 106 human participants (56.6%) harbored a breeding population of lice (i.e., contained at least 1 adult female and 1 adult male louse). This suggests that human louse populations experience slow, measured rates of growth. Several adaptations may account for slow growth and genetic homozygosity of louse populations on humans.

First, morphologic studies suggest that fecundity in *P. humanus* is constrained by female anatomy. When compared with mosquitoes (an insect capable of undergoing explosive population growth), Keilin and Nuttall (1930) found that the average size of spermathecae in adult *P. humanus* females was quite small relative to the average size of their ovaries. Thus, the capacity for louse spermathecae to house large or multiple spermatophores (i.e., multiple matings) appears limited (Mukerji and Sharma, 1951). The limited capacity for sperm storage may explain why most mated female *P. humanus* lose the ability to fertilize eggs within 20 days (Bacot, 1917). Without an influx of new adult males, the breeding potential of female-only populations may have to await the sexual maturation of nymphs (which may or not be their offspring). This may contribute to smaller population size as well as population inbreeding and homozygosity.

Second, the unusual inheritance system of "paternal genome elimination" in adult male *P. humanus* may also contribute to a higher-than-expected homozygosity in head and body lice. In this system, adult male lice fail to incorporate paternal chromosomes into the sperm during spermatogenesis and pass on only maternally derived chromosomes to their offspring (McMeniman and Barker, 2005; De La Filla et al., 2018). The fact that *P. humanus* has an unusual mode of inheritance was observed over 100 yr ago. In a series of mating experiments (e.g., 60 crosses), Hindle (1917) noted that the resultant offspring were either mostly or entirely female or mostly or entirely male. Thus, the peculiar mode of inheritance of *P. humanus*, coupled with its limited sperm storage and relatively small breeding populations, could act together to reduce the overall size and genetic diversity of louse infrapopulations on humans.

Another contributing factor to small, homozygotic populations may involve the sex ratio. The overall sex ratios of 567 head lice and body lice examined during our 3-yr sampling period showed a consistent female bias (Fig. 1). Significant female-biased sex ratios were also reported for head louse populations in Argentina (Perotti et al., 2004) and for 5 species of Ischnocera and Amblycera chewing lice of birds (Szczykutowicz et al., 2006; Ahmad et al., 2010). However, another study examining lice of seagulls (González-Acuña et al., 2011) and 2 classic studies examining human head lice from a wide geographic range (e.g., Africa, Australia, England, India, Sri Lanka) with very large sample sizes (>870 infested participants; 11,197 adult lice examined) (Buxton, 1941; Nuttall, 1919) concluded that the proportion of females to males differs significantly from equality, but with an excess of males occurring in 1 place and of females in another. Thus, it may be inappropriate to view the sex ratio in *P. humanus* as a purely fixed attribute. The sex ratio may fluctuate within populations over time and space.

This survey confirms the findings of Sasaki et al. (2006) that head lice in Nepal can be infected with *B. quintana* (Table II). Traditionally, only body lice were believed to be involved in the transmission of bacterial pathogens causing louse-borne typhus (*Rickettsia prowazekii*), relapsing fever (*Borrelia recurrentis*), and trench fever (*Bartonella quintana*). Recent studies using PCR-based methods have called this into question and have reported *B. quintana* DNA in head lice from various parts of the world (Sasaki et al., 2002, 2006; Bonilla et al., 2009; Angelakis et al., 2011; Boutellis et al., 2012; Sangaré et al., 2014). Our study identified 3 participants who harbored *B. quintana*-positive lice (Table II). In each case, only a single louse (i.e., 7 to 20% of the louse population) was positive, demonstrating that louse infrapopulations may contain a mix of infected and noninfected lice. It is not an all-or-nothing situation.

The detection of *B. quintana* DNA in head lice does not necessarily prove head lice are competent vectors for that pathogen. The vector competence of head lice for *B. quintana* has recently been shown in laboratory studies to be considerably less than that of body lice (Kim et al., 2017). Fecal shedding of viable *B. quintana* bacteria by head lice was several-fold less than for similarly infected body lice. Reduced vector competence of head lice was attributable to the vigorous transcription of immune effectors (e.g., defensins) in the midgut of head lice.

In conclusion, this report describes the population structure of head and body louse infestations of 106 people in Pokhara, Nepal. Head lice were more prevalent than body lice, although a substantial proportion of infested people (15%) harbored both head and body lice concurrently. Louse populations were usually small (≤10 lice per person), composed mostly of nymphs, with adults being

increasingly female biased with increasing population density. Further studies are needed to determine the dynamics of person-to-person transmission of lice to identify the factors that contribute to the spread of pediculosis among people.

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