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HEAD LOUSE PALEOEPIDEMIOLOGY IN THE OSMORE RIVER VALLEY, SOUTHERN PERU

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KEY WORDS

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ABSTRACT

Recent studies of louse ectoparasites from mummies have developed robust data sets that allow a true epidemiological approach to the prehistory of louse parasitism. One epidemiological principle is that the binomial of overdispersion is normally negative, meaning that in a host population, parasites are aggregated in a few individuals. We demonstrate the overdispersion of lice in 3 different prehistoric communities that differ along 3 axes or variables: environmental setting, socioeconomic status, and cultural affiliation. Distinct cultural practices could have been involved in different patterns of louse infestation. Prevalence, intensity, and abundance of infestations exhibit statistically significant differences between the communities. We also find differences in prevalence between subadults and adults that contrasted by cultural affiliation and suggest conditions different from those seen today. We show that overall prevalence was affected primarily by ecological setting, not socioeconomic status nor cultural affiliation. These findings demonstrate that statistical analysis of archaeological data can reveal the states of infestation in past populations with lifestyles not seen in modern people. Our approach paves the way for future comparisons of subpopulations within archaeological communities.

"Mortui viventes docent," meaning "the dead teach the living," is the theme of the Paleopathology Association. This is especially true for archaeological parasitology, through which the details of parasite–human interaction can be revealed from remote populations and extinct lifestyles. The application of parasitological principles to archaeological samples results in quantitative data that is epidemiologically significant (Martinson et al., 2003; Reinhard and Buikstra, 2003; Reinhard, 2017; Camacho et al., 2018; Morrow and Reinhard, 2018; Camacho and Reinhard, 2020). Studies of parasites in archaeological remains, especially lice from mummies, have developed robust data sets that allow a true epidemiological approach to be applied to the prehistory of louse parasitism (Reinhard and Buikstra, 2003; Arriaza et al., 2012, 2013a, 2013b, 2022). One of these approaches involves demonstrating that archaeological populations conformed to the principle of parasite overdispersion and comparing the degree of overdispersion across populations (Reinhard and Buikstra, 2003).

There are 2 ecotypes of *Pediculus humanus*: body lice, *Pediculus humanus humanus*, and head lice, *Pediculus humanus capitis*, as recently reviewed (Amanzougaghene et al., 2020). In this paper, we focus on prehistoric Andean head lice. The head louse lives, breeds, and lays its eggs at the base of hair shafts and blood feeds every 4–6 hr. Lice are highly host specific and therefore can provide unique data with which to reconstruct human migration and human evolutionary history, augmenting fossil records. In general, phylogenetic analyses indicate that human and chimpanzee lice shared a common ancestor some 6 million years ago. For more recent times, louse genetic data trace a human demographic diaspora beginning roughly 100,000 yr ago. This corresponds to paleontological and archaeological evidence of the out-of-Africa dispersion of modern humans. Most relevant to this paper, these data suggest the timeframe for the peopling of the New World (Amanzougaghene et al., 2020).

Previous genetic analyses of human head lice in our research area revealed which louse clades entered the New World. Analysis of Chiribaya mummies from the Osmore Valley revealed that head lice belonged to clade A (Raoult et al., 2008); this is the same population addressed in the present paper. From Camarones, Chile 312 km to the south, analysis of a 4,000- yr-old mummy identified both clades A and B on the same individual (Boutellis et al., 2013).

Population studies of mummies offer the potential to discover new aspects of louse infestation. For example, although modern head louse infestation is associated mostly with children, analysis of Chiribaya mummies showed that infestation was primarily a feature of adulthood (Reinhard and Buikstra, 2003; Arriaza et al., 2012; Reesor, 2021). In this paper, we further pursue this theme of louse paleoepidemiology.

Although head louse infestation is one of the most prevalent parasite conditions in human populations (Clark et al., 2013), the epidemiological study of pediculosis in modern human populations is somewhat ignored, with almost all studies related to prevalence in small populations (Amr and Nuiser, 2000; Catalá et al., 2005; Lesshafft et al., 2013). The paleoepidemiological analysis of past populations might provide case studies of the occurrence of these parasites in conditions that no longer exist, to be compared to modern populations.

The prehistoric Andes is an example of infection conditions that have no counterpart today. For Inca times, there was a cultural tolerance to head lice. When there was no other way for a community to contribute taxes, lice were presented as tribute (Arriaza et al., 2022). This worldview contributed to its high prevalence, and this pattern could have applied to earlier Andean periods.

Overdispersion refers to the phenomenon of aggregation of a majority of parasites in a minority of that parasite's host population. Thus, the majority of hosts have few or no parasites, while a small number of hosts carry a great number of parasites. In parasitological terms, this phenomenon is best described by the negative binomial distribution (Anderson, 1993). Crofton (1971) showed that overdispersion was present in parasite populations. Since then, parasite overdispersion has been documented among a variety of vertebrate and invertebrate hosts (Croll and Ghadirian, 1981; Crompton et al., 1984; Anderson and May, 1985; Shaw and Dobson, 1995; Shaw et al., 1998). Poulin (2007) explored the potential that there are general laws in parasite ecology. For a "law" to exist, he argued that there must be a predictable, recurring ecological pattern. Overdispersion appears to be one such "law" in parasitology. Given the apparent universality of overdispersion among parasites, we should be able to observe it in archaeological samples.

Ectoparasites from mummies are particularly important in understanding the epidemiology of parasitism. Lice are obligate, species-specific parasites that are expected to conform to models of overdispersion and other epidemiological principles. Previous studies have identified morphologically *Pediculus humanus capitis* nits and eggs cemented to the hair shafts of people in life that remained there after death (Ewing, 1924; Araújo et al., 2000; Arriaza et al., 2012, 2013a, 2013b, 2022; Reinhard et al., 2020). The nits and eggs on the hair shafts of mummies are a permanent record of infestation at the time of host death and for a few weeks before death (Reinhard and Buikstra, 2003). The nits and eggs are easily quantified on mummy hair and these data can be used to estimate louse burden (Reinhard et al., 2020).

Archaeological population studies of louse infestation can be used to explore overdispersion in prehistory (Reinhard and Buikstra, 2003; Arriaza et al., 2013b). In 2003, Reinhard and Buikstra studied mummies of the Chiribaya culture of Peru, quantifying louse infestation on an individual basis by calculating the maximum number of eggs and nits cemented to hair shafts on the scalps of 146 mummies. A companion paper documented a likely source of infection with Chagas disease and reviewed other infections (Martinson et al., 2003). To validate the paleoepidemiological utility of archaeological parasite data, overdistribution had to be demonstrated. As expected, the distribution of nits and eggs on Chiribaya hosts reflected a negative binomial of overdispersion (Reinhard and Buikstra, 2003). This finding supported the statistical value of parasitological data when large numbers of human remains can be evaluated.

Table I. Characteristics of the 3 sites.

Site	Location	Social status	Culture
Algodonal	Coast	Low	Ilo-Tumilaca/Cabuza
Chiribaya Alta	Coast	High	Chiribaya
Yaral	Inland	Low	Chiribaya

Combining the data from Reinhard and Buikstra (2003) with more recently obtained archaeological data on the mummies, especially from additional individuals from the site of Algodonal (Owen, 1993), we can now begin to evaluate how demographic and social variables may have affected the prevalence and overdispersal of parasites. Specifically, we analyze patterns of louse infestation in mummies from 3 archaeological sites in the Osmore River valley in southern Peru (also called the valley of Moquegua or, near the coast, the Valley of Ilo). The 3 sites are roughly contemporaneous, spanning broadly about cal AD 900 to 1400. Each differs from the other two in just 1 of 3 axes of variation, providing information on each axis, as summarized in Table I. Algodonal and Chiribaya Alta are located in the coastal segment of the Osmore River valley, while Yaral lies much further inland at higher elevation and usually outside the coastal fog belt. This grouping provides a contrast on an ecological axis. Yaral and Algodonal were settlements of relatively low-status farmers who were buried with just a few modest goods, while Chiribaya Alta appears to have been a regional center where people were buried with relatively lavish offerings. This grouping provides a contrast on an axis of social status. Finally, Chiribaya Alta and Yaral were occupied by people of the Chiribaya culture, which dominated these portions of the Osmore Valley, while Algodonal was occupied by people of the very different Ilo-Tumilaca/Cabuza (ITC) culture, who were immigrant refugees and their descendants from the collapse of the Tiwanaku state further inland. This grouping provides a contrast on an axis of cultural affiliation. The Ilo-Tumilaca/Cabuza and Chiribaya groups were culturally distinct in the style of their ceramics, wooden spoons, clothing, and house construction. Cultural affiliation might be expected to affect epidemiology. For example, the 2 populations' diets differed, and Chiribaya families lived in dense communities of large, walled residential compounds with complicated, restricted floor plans, while Ilo-Tumilaca/Cabuza people lived in small, freestanding houses of one or a few rooms (Owen, 2005).

The distinct characteristics of the 3 sites allowed us to assess possible patterning in lice infestations along 3 axes or variables: coastal vs. inland location and environment (an ecological axis), high vs. low socioeconomic status (a social status axis), and cultural practices of the dominant, established Chiribaya vs. the immigrant, refugee Ilo-Tumilaca/Cabuza people (a cultural affiliation axis). Finally, we also compared infestation patterns between the sexes and across age groups in the entire sample and within the population from each site to see if basic demographics affected parasitism.

MATERIALS AND METHODS

This research was facilitated by Programa Contisuyo, established in 1982 as a multidisciplinary Peruvian–American collaboration for the study of Andean prehistory in southern Peru. Dr. Michael Moseley of the Field Museum of Natural History and the University of Florida and Dr. Fernando Cabieses of the Consejo Nacional de Cultura, Insituto Nacional de Cultura, founder of the Museo Peruano de Ciencias de la Salud, and the first director of the Museo de la Nación, were instrumental in establishing the program and recruiting numerous other institutions in both countries. Southern Peru Copper Corporation [SPCC] underwrote Programa Contisuyo from its inception. Programa Contisuyo was an umbrella organization that provided logistical support, including housing and lab facilities through SPCC, for numerous research projects with their own grants from sources including the National Science Foundation, Fulbright-Hays Program, Pritzker Foundation, Wenner-Gren Foundation, H. John Heinz III Charitable Trust, and many others, executed by teams of United States, Peruvian, and other archaeologists, students, and technicians. A shared theme was evaluating cultural interchange between populations at different elevations in the Andes. The study of human remains was central to understanding highland, mid-valley, and coastal societies. The Chiribaya bioarchaeological project, directed by Jane Buikstra, began in 1989 with open doors to many Peruvian researchers and students (Lozada, 2014). The Proyecto Colonias Costeras de Tiwanaku, directed by Bruce Owen, was a dissertation project whose multinational team conducted excavations and surveys from 1989 through 1991. In 1992, the field house and lab established by the 2 projects became the Centro Mallqui conservation center and museum, a nonprofit organization dedicated to the conservation, study, and educational presentation of cultural resources of Perú, where the remains reported on here are stored. The Centro Mallqui is directed by Sonia Guillén.

The archaeological sites

The Osmore drainage is the fourth southernmost river system of the many that flow southwest down the Pacific slope of the Andes in Peru, traversing the northern extension of the Atacama desert to empty into the Pacific Ocean near Ilo, Peru, about 150 km northwest of the border with Chile (Fig. 1). It has 4 distinct zones: the upper valleys, the middle valley, a dry gorge, and the lower, coastal valley (Owen, 2005). The upper valleys are composed of confluences of canyon tributary valleys that descend from highland grasslands. Some of these valleys are terraced for irrigation. Two prehistoric cultures controlled parts of the upper and middle valleys beginning about 1,500 yr ago. The Wari culture, expanding from the highlands far to the northwest, established several defensible towns, primarily in the upper valleys. Around the same time, the Tiwanaku culture began to colonize enclaves in valleys of the Pacific slope of the Andes, including the middle Osmore Valley, from its capital by Lake Titicaca.

The middle valley comprises 26 km of valley-bottom farmland surrounded by extremely dry desert slopes. Tiwanaku people occupied this area from around 1,500 yr ago, primarily at a few large towns such as the monumental temple center of Omo, the agricultural entrepot of Chen Chen, and the farming settlement of Rio Muerto as well as at a few smaller settlements.

The Osmore River flows underground for 31 km downstream from the middle valley. This area is characterized by a deep dry gorge that is surrounded by desert. The unpopulated gorge isolates the coastal valley from the middle valley.

In the fourth zone, the river reemerges as a surface stream near the Pacific coast. It forms a coastal valley with a narrow, arable floodplain. In modern times before the recent Pasto Grande irrigation project, the river ran on the surface for only a few days or weeks each year. Archaeological evidence indicates that it flowed year-round in prehistory. The coastal valley was occupied by indigenous agriculturalists that developed the socially stratified Chiribaya culture. They were established by AD 770 to 900 and persisted until after AD 1350 (Owen, 2005). The Chiribaya subsistence economy was based on fishing, agriculture, and herding (Lozada et al., 2005; Owen, 2005; Knudson et al., 2007).

The Tiwanaku polity collapsed around AD 1000, causing a dispersal of people into regions well beyond Lake Titicaca and Tiwanaku's former colonies. Some settled in the coastal valley near established Chiribaya towns as a distinct, lower-status minority. In the coastal Osmore Valley, these immigrants are known as the Ilo-Tumilaca/Cabuza culture (Owen, 2005; Knudson and Price, 2007).

We collected and analyzed the louse infestation data from prehistoric mummies from the Osmore Valley. The history of excavation of the sites and earlier parasite analyses are summarized by Martinson et al. (2003), Reinhard and Buikstra (2003), and Reinhard et al., (2020). The archaeology has been extensively described (Lozada et al., 2005; Owen, 1993, 2005; Knudson et al., 2007). A total of 171 mummies were available from 3 sites for analysis. Of these, 117 were sufficiently preserved for quantitative analysis: 32 from Algodonal, 64 from Chiribaya Alta, and 21 from Yaral.

The 2 sites from the coastal valley represent socioeconomic extremes. Although excavations of cemeteries of Chiribaya Alta were funded, excavations of domestic areas there were not. This inhibits defining the exact function of Chiribaya Alta within the larger society, although we can extrapolate from copious evidence on the surface and extensive domestic and mortuary excavations at other Chiribaya sites. Chiribaya Alta was a population-dense town, perhaps an administrative center, home to many high-status people, and likely the center of the complex Chiribaya economy. It was apparently a regional center for the burial of large numbers of high-status individuals with numerous, fine, and diverse burial furnishings including agricultural goods, bags of coca leaves, ceramics, clothing, and tools representing the decedents' occupations. Many other Chiribaya cemeteries and burials within domestic areas have been excavated; the offerings and practices were similar, but typically fewer and less elaborated. The second coastal valley site is Algodonal, a smaller settlement with remains of a probably initial Ilo-Tumilaca/Cabuza occupation, probably followed by a more intensive Chiribaya one and an adjacent cemetery that was used only by Ilo-Tumilaca/Cabuza immigrants. These appear as a group to have been relatively disadvantaged in comparison to most Chiribaya people, perhaps reflecting their intrusive, immigrant, or refugee status. Their burial offerings are typically fewer in quantity and poorer in quality than those from Chiribaya Alta or other, less-elite Chiribaya

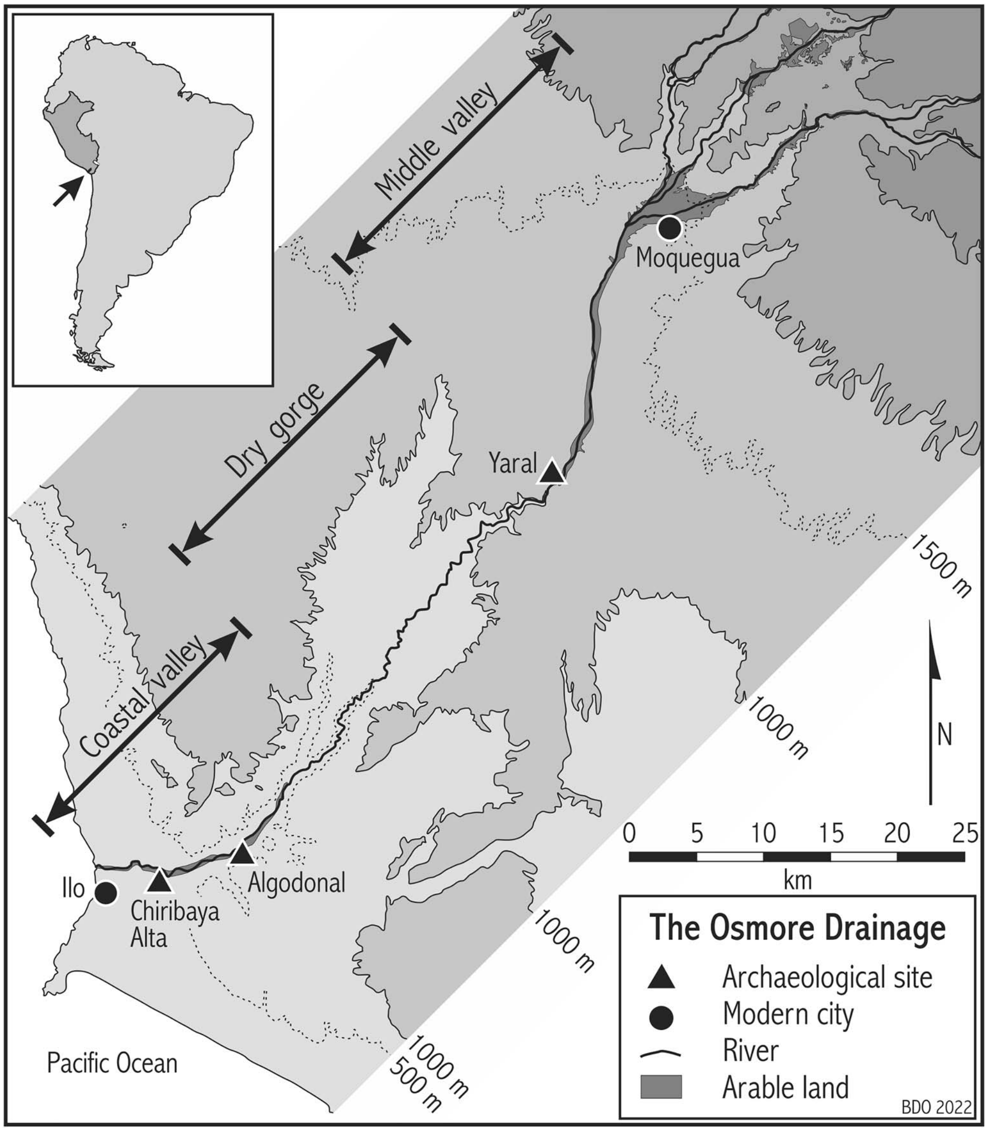

Figure 1. Map showing location of Yaral in the middle valley of the Osmore drainage and Chiribaya Alta and Algodonal in the coastal valley. Yaral and Chiribaya Alta are of the Chiribaya Culture. Algodonal is affiliated with the Ilo-Tumilaca/Cabuza Culture.

villages. Domestic excavations at Algodonal and another Ilo-Tumilaca/Cabuza site nearby (Loreto Alto) found the houses to be smaller, simpler in plan, and less solidly constructed than those at Chiribaya sites.

The middle-valley site of Yaral was a large town with over 300 residential terraces, 2 identified cemeteries, and 2 large, communal buildings with stone foundations. Burials at Yaral are characterized by modest quantities of usually simple offerings of utilitarian items. The range of wealth implied by the Yaral burial assemblages is limited and does not approach that of Chiribaya Alta.

Data collection

Mummy tissues and hair are extremely fragile. The hair was unusually brittle at the time of analysis. If extreme care is not taken, hair can separate from the scalp and braided hair can separate from basal hair adherent to the skin.

Mummy scalp and hair come in variable conditions due to scalp-specific taphonomy within mummy bundles. Although the scalp consists of 5 layers (skin, connective tissue, epicranial aponeurosis, loose areolar tissue, and pericranium), the upper 3 layers exist as a single unit. This unit merges with occipitofrontalis muscle groups. In our observations, taphonomic processes within the mummy bundle affect the scalp structures. (1) In some cases, the entire scalp, hairstyle, and internal layers remain articulated with the skull. (2) However, there is a tendency for the surface of the scalp skin to shrink, perforate, and even tear within the bundle. This often results in the separation of hair from the skin. (3) In other cases, the dense connective tissue layers of the scalp separate from the skull as the loose areolar tissue decomposes. In these cases, the scalp and hair separate as a unit from the skull. (4) In rarer cases the hair separates from the scalp and the scalp separates from the skull. We developed our method to quantify lice to facilitate the collection of consistent data under these variable conditions (Figs. 2, 3).

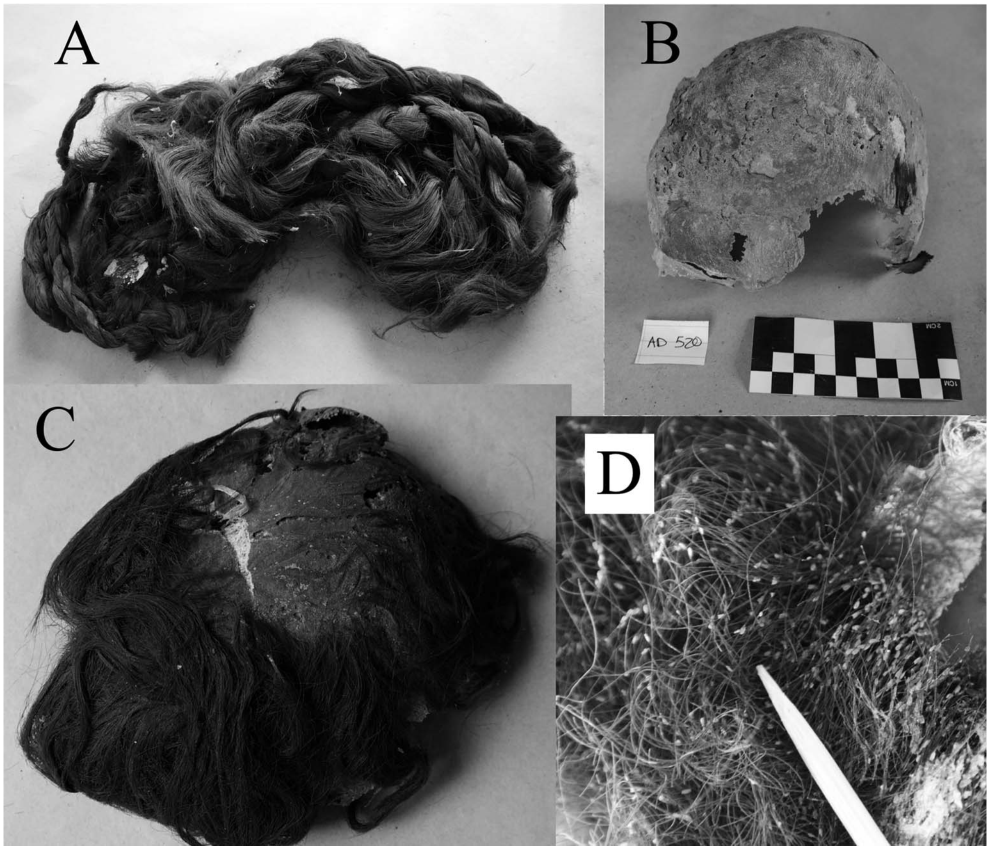

Figure 2. (**A**) Plaited hair styles of interwoven braids are heavy relative to the dried scalp tissue. Therefore, these styles separate as a unit. Quantification can still be accomplished on the hair shafts of the braids and basal hair that remains fixed on the skin. (**B**) In this case, the hair separated from the scalp and the skull separated from the skull. In such cases, it is sometimes not possible to include such remains in the sample. Note the large pores that open in the skin as desiccation progressed. (**C**) This infested example illustrates tearing and pitting associated with desiccation. (**D**) This illustrates an infestation still quantifiable on a separated scalp. Images are from analyses in the Centro Mallqui, Ilo, Peru.

Methods were guided by conservation principles consistent with indigenous sensibilities. Peruvians were included in the excavation and analysis. Lab staff and conservation specialists were Peruvian, and assistants were employed from the local population. The louse analysis was done in the conservation lab with abundant help to clean the hair and scalp. The lab was open and visitors occasionally stopped by to see the mummies and work progress. Some of the visitors were likely descendants of the Chiribaya people. Discipline in exhibiting clear respect for the mummies and absolute care for the hair and scalp preservation was maintained. Taphonomic issues created fragile remains that had to be respected and preserved so that the remains were left in the same condition after analysis that they were in before analysis. Remains that were simply too fragile for study were not included in the sample.

The initial tranche of data was collected in 1990, and a second tranche used the same methods in 2013. The fragility of mummy hair and scalp precluded using some clinical and forensic methods current in 1990. We could not use combs because that would break the hair. We could not crop the hair or make samples of full hair lengths because that was counter to the goal of conservation. We were challenged by the question: how can we quantify louse infestation while preserving the specimens? The 1 factor available in abundance was time. We could expend hours per mummy to assess infestation to ensure that no damage was done to the specimens by careful, delicate processes of exposing and recovering infested areas.

We collected data from 2 general categories of host substrate: hair bases and adjacent scalp, and hair shafts 4–6 cm from the scalp (Fig. 3). Our approach was generally consistent with modern methods but with a priority focus on conservation (Borges and Mendes, 2002; Gairí et al., 2007; Heukelbach, 2010). Mummy heads were examined by gingerly lifting the hair at normal areas of infestation, over the ears in the temporal areas, and at the occipital area at the back of the head. Once these areas were exposed, a flexible cardboard template with a 2 × 2-cm aperture was placed over the exposed regions. The aperture was cut in a flexible 5 × 5-cm square of thin, matt cardstock. This template standardized the sample area and focused attention on a specific area for counting while gently maintaining the hair in articulation with the scalp by light pressure on the 5 × 5-cm area. All nits and eggs at the scalp in the 2 × 2-cm sample area were counted. Then, hair shaft sample areas 4–6 cm from the scalp were examined for areas of maximum and minimum infestation. Again, the flexible template was applied to the hair to standardize the sample area and focus counting while maintaining the preservation of individual hairs and the hair style overall. Twelve nonoverlapping sample areas were observed on each mummy with

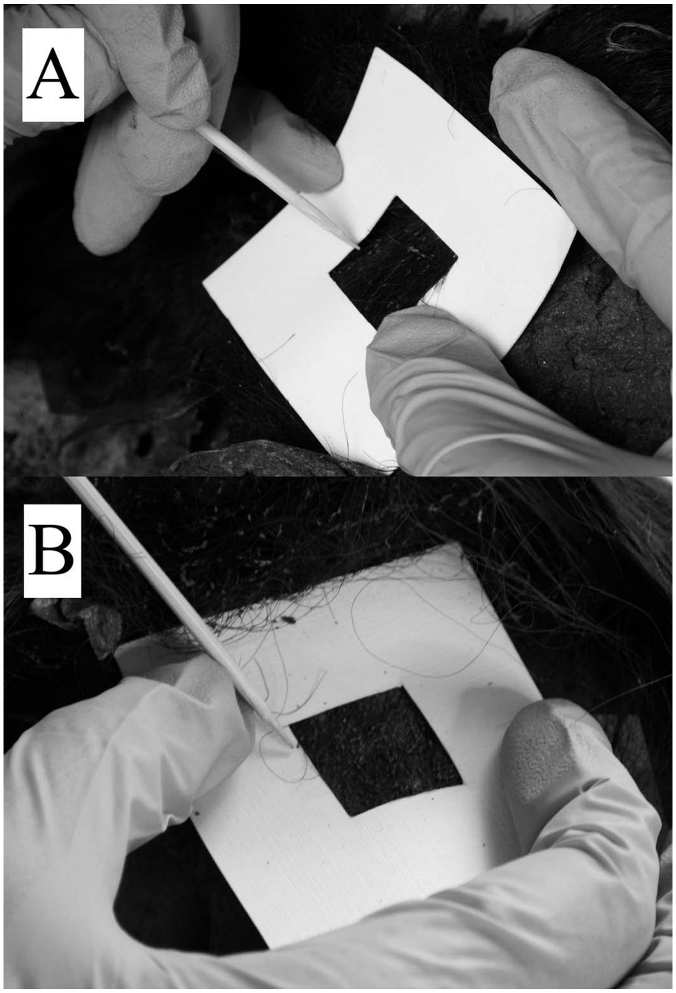

Figure 3. The flexible matt surface template was ideal for quantification. Its flexibility could conform to the specimen shape with gentle pressure. Also, it could be easily and harmlessly inserted under long hairstyles to document infestations at the scalp. (**A**) In this case, the template is being used to count lice on a concave surface of a separated hair and scalp specimen. (**B**) Ideally, quantification was facilitated by intact hair preserved in articulation with the mummy, as in this case. Using a bamboo probe allowed counting nits/eggs in depth. The probe was used to gently separate the hair to see nits/eggs below the upper hair shafts and then to restore the original arrangements of the shafts. Images are from analyses in the Centro Mallqui, Ilo, Peru.

sufficiently preserved scalp and hair, recording the count of nits/eggs in each. Six sample areas were attempted at hair bases and 6 on hair shafts. For analysis, the maximum count average from 3 observations was used (Reinhard and Buikstra, 2003). This method has become standard for louse analysis in the region. Arriaza et al. (2013b, 2022) based their work on Reinhard and Buikstra (2003). Of the methods applied to archaeological remains as recently summarized and illustrated (Reinhard et al., 2020), this method is the best for quantifying lice on mummies. The fact that all current researchers in archaeological Andean pediculosis use the same methods results in a growing body of comparable data (Arriaza et al., 2022).

Complete results were obtained from all Yaral mummies. For 13 Chiribaya Alta and 17 Algodonal mummies, taphonomic processes resulted in decomposition of scalp surfaces, resulting in hair separation. Therefore, scalp observations were not obtained for these individuals but hair observations were accomplished. In addition, 1 adult male from Chiribaya Alta had his hair shorn very close to the scalp. This noteworthy mummy had the highest scalp louse infestation and pronounced resorption of the bone of the maxillary hard palate, ethmoid, and with complete exposure of the maxillary sinuses (Martinson et al., 2003:fig. 9). Therefore, for this mummy no hair observations could be made.

The mummies were divided into 3 age categories. For Algodonal, the divisions were infant (n = 6), subadult (n = 3), and adult (n = 22). The original 1991 database compiled for Chiribaya mummies (Reinhard and Buikstra, 2003) recognized adult and subadult as demographic categories, but not infants as a separate category. Thus, mummies from Chiribaya Alta were divided into subadult (n = 36) and adult (n = 32). Mummies from Yaral were divided into subadult (n = 14) and adult (n = 7). Five mummies from Yaral were identified as male and 2 as female. Thirteen mummies from Chiribaya Alta were male and 19 were female. Five from Algodonal were definitely male and 12 definitely female. The complete data sets for Chiribaya Alta and Yaral were published (Reinhard and Buikstra, 2003: table 2). The data for Algodonal are available in Suppl. Table S1.

Statistical analyses

We combined all lice counted on each mummy to represent that individual's total abundance of lice. Because some mummies could be assessed only at the scalp or only in the hair, we also analyzed the number of lice or nits found at these 2 anatomical locations separately. We summarized these data for the mummy population of each archaeological site in 3 ways. Prevalence is the percentage of all mummies in the population on which lice and/or nits are present. Mean intensity is the mean number of lice and nits on those mummies that are infested, measured in maximum nits or eggs/cm^2. Mean abundance is the mean number of lice and nits on all mummies, infested or not, measured in nits or eggs/cm^2. We report prevalence, mean intensity, and mean abundance on the scalp, hair, and overall (in scalp, hair, or both) for each site's population of mummies. The means are provided in deference to long-standing practice but should be treated with care (Reiczigel et al., 2019).

To verify the overdispersion of lice for each site analyzed, we measured Poulin's discrepancy index, the negative binomial exponent (k), and the variance/mean ratio for each. Poulin's discrepancy index measures the discrepancy between the observed distribution of parasites in hosts and a uniform distribution, where D = 0 indicates a uniform distribution and D = 1 indicates all of the parasites concentrated in a single host. We also compared the mean abundance and mean intensity among sex and age groups and between sites using Neuhauser's location test. These distribution and overdispersion analyses were performed using the software Quantitative Parasitology v.1.0.13 (QPWeb) (Reiczigel et al., 2019, 2020).

We assessed the significance of differences in prevalence between mummy populations in 2 × 2 contingency tables using Barnard's unconditional exact test (Boschloo's variant) reporting 2-tailed probability values. Barnard's unconditional test is more appropriate than the more commonly used Fisher's (conditional) exact test for this research design because the sample sizes were fixed in advance, but the total number of infestations was

Table II. Prevalence, intensity, and abundance of louse infestations by site and host substrate.

Site	Host substrate	No. assessed	No. infested	Prevalence	Mean intensity	Mean abundance
Algodonal	Scalp	15	5	0.33	81.4	27.1
	Hair	31	12	0.38	41.8	15.7
	Scalp or hair	31	13	0.41	67.2	27.3
Chiribaya Alta	Scalp	50	19	0.38	16.8	6.4
	Hair	63	20	0.32	6.6	2.1
	Scalp or hair	64	25	0.39	18.1	7.1
Yaral	Scalp	21	4	0.18	27.2	5.0
	Hair	21	2	0.09	6.0	0.5
	Scalp or hair	21	4	0.18	30.2	5.5

determined by observations (Ludbrook, 2008; Lydersen et al., 2009; Calhoun, 2019a, 2019b; Reiczigel et al., 2019). Prevalence analyses using Barnard's test were performed with R (R Core Team, 2020). Given the small sample sizes, we consider *P*-values less than or equal to 0.10 to be suggestive and those less than or equal to 0.05 to be significant.

RESULTS

Table II summarizes the number of mummies assessed, number infested, prevalence, mean intensity, and mean abundance for scalp, hair, and both for each of the 3 sites.

Overdispersion, intensity, and abundance

The overdispersion analysis, summarized in Figures 4–6 and Table III, shows that infestations at all 3 sites have a negative binomial distribution,with small values of the exponent k, have high values of Poulin's discrepancy index (D), and have high variance/mean ratios (Figs. 4–6; Table III), all indicating overdispersion. Some sample sizes were too small to permit calculation of k.

Patterns in louse infestation prevalence

Prevalence of louse infestation was lower at Yaral than at either of the other 2 sites individually (Table II). Mummies from Yaral had significantly lower prevalence on hair than did those from either other site at the 5% confidence level, lower prevalence overall than did those from either other site at the suggestive 10% level, and lower prevalence on the scalp than did those from Chiribaya Alta at the suggestive 10% confidence level (Table IV). By contrast, prevalence at Chiribaya Alta and Algodonal in hair, scalp, or overall was indistinguishable (Table IV). Patterning appears stronger on hair than scalp, probably because the very small sample of infested individuals from Yaral happens to include 4 scalp infestations but only 2 hair infestations (Tables II, VI).

In order to assess the effect of each of the 3 study axes or variables (location or ecological setting, social status, and cultural affiliation) on the prevalence of louse infestation, Table VI groups the data in 3 ways, each contrasting a different axis or variable. Table VI shows that we found no remotely significant difference in site-level prevalence by socioeconomic status of the site, nor by cultural affiliation. Location or ecological setting,

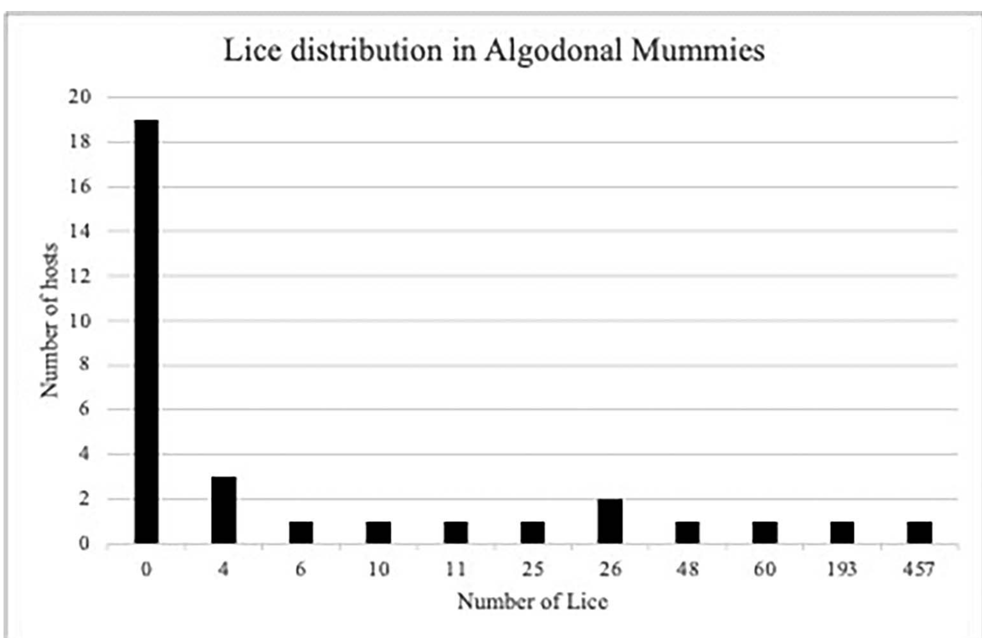

Figure 4. Overdispersion of lice among mummies from Algodonal.

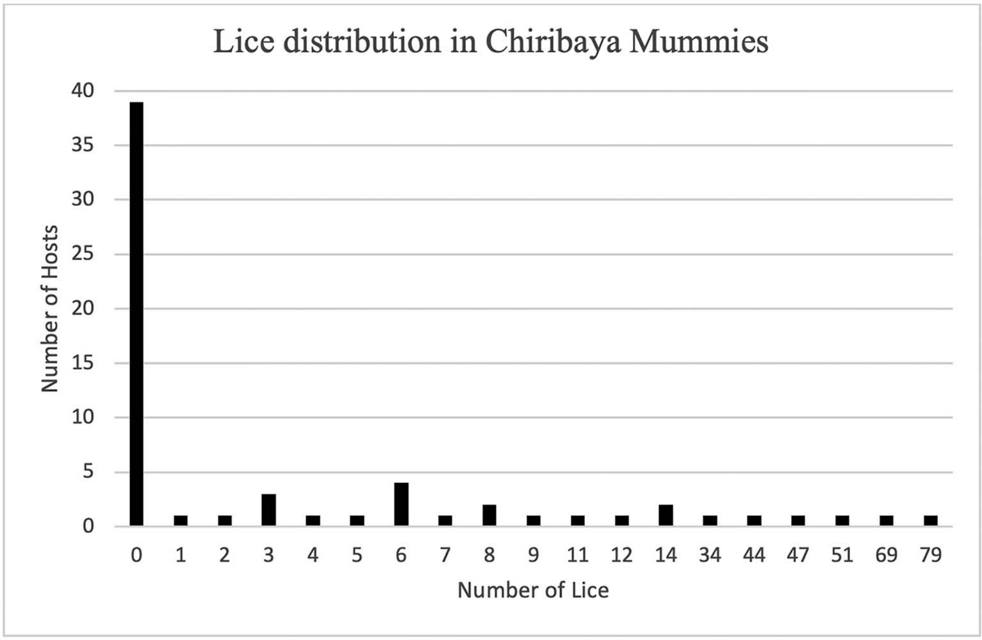

Figure 5. Overdispersion of lice among mummies from Chiribaya Alta.

however, did have a significant effect. Prevalence was significantly higher in the two coastal valley populations than at Yaral in the middle valley, with louse infestations in coastal populations apparently about twice as common as they were inland at Yaral (Tables V, VI).

Table VII breaks down the prevalence of louse infestations by demographic variables of sex and age group within each mummy population and in the sample as a whole. Table VIII assesses the significance of differences between demographic categories within each site, within the 2 coastal sites combined, and in the sample as a whole. Table IX assesses the significance of differences between sites within demographic categories. We found no significant differences by sex or age group within the Algodonal, Yaral, or combined coastal populations, but at Chiribaya Alta, louse infestation was significantly more prevalent among adults than among subadults, at the 5% confidence level (Tables VII, VIII). The same was true of the entire sample, albeit only at a "suggestive" level of confidence, presumably due to the impact of the large Chiribaya Alta sample (Tables VII, VIII). Comparing the 3 populations with each other, we found no differences in

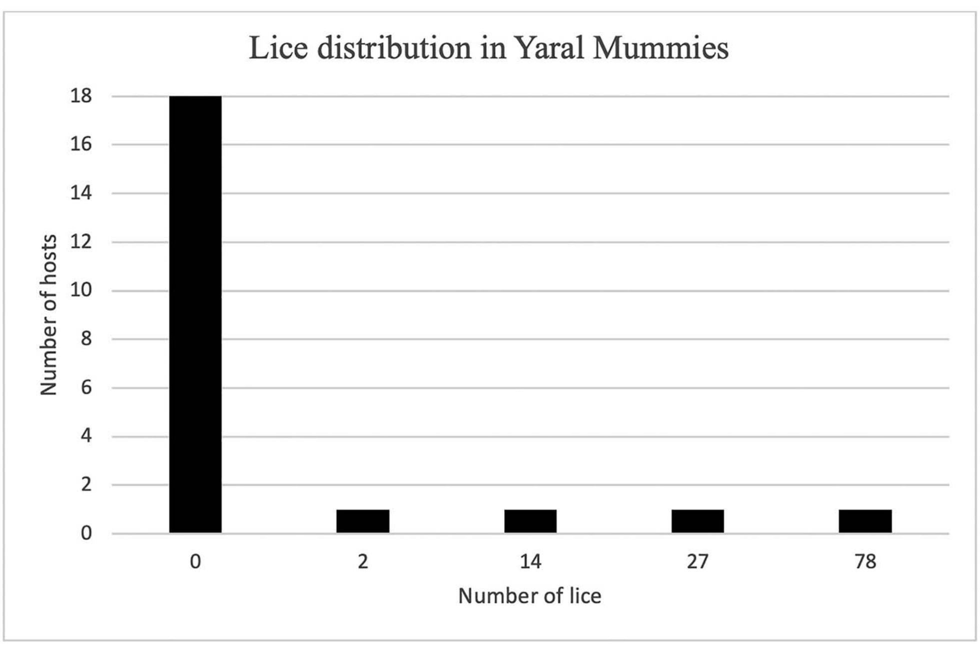

Figure 6. Overdispersion of lice among mummies from Yaral.

Table III. Overdispersion values for the 3 sites.

Site	Poulin's discrepancy index (D)	Variance/mean ratio	k
Algodonal			
Hair	0.842	143.2	0.0962
Scalp	0.783	139.7	NA*
Chiribaya Alta			
Hair	0.811	11.4	0.1457
Scalp	0.846	42.0	0.1199
Yaral			
Hair	0.906	10.1	NA*
Scalp	0.865	46.4	NA*

* NA = Small sample size, k could not be calculated.

prevalence among males, females, or all adults from 1 site to another (Tables VII, IX). However, subadults at Algodonal had higher infestation prevalence than did subadults at Yaral (significant, $P = 4.2\%$) or Chiribaya Alta (suggestive, $P = 7.7\%$) (Tables VII, IX).

In order to assess the effect of each of the 3 study axes or variables (location or ecological setting, social status, and cultural affiliation) on the prevalence of louse infestations by sex and age group, Table X again groups the data in 3 ways, each contrasting on a different axis or variable. Table XI shows that the only demographic group whose louse infestation prevalence is clearly affected by any of the 3 axes is subadults, including infants, which have a significantly higher infestation prevalence—over twice as high—in Ilo-Tumilaca/Cabuza settings than in Chiribaya ones ($P = 3.7\%$).

We found no significant differences in prevalence between scalp and hair substrates in any of the mummy populations, the coastal populations combined, or the entire sample (Table VIII). There is no significant difference in infestation in a given substrate between the sites (Table IV).

DISCUSSION

Overdispersion was evident in all samples, with an aggregation of a majority of louse nits/eggs on a minority of hosts, as expected of louse distribution (Reinhard and Buikstra, 2003; Arriaza et al., 2012). Table III provides the values of the variance/mean ratio, Poulin's discrepancy index (D), and the negative binomial exponent (k). The similar high values of D in each mummy population indicate a high and similar degree of overdispersion in each. The variance/mean ratio also reflects the distribution of parasites, where a value near 1 indicates a random distribution and higher values indicate a distribution that is more narrowly clumped. While the observed variance/mean ratios in the 3 mummy populations differ, they are all very high, as expected in cases of overdispersion. Finally, the exponent k of the negative binomial distribution models the degree of aggregation of parasites in hosts, where low values of k indicate high aggregation. The sample size from some sites was too small to estimate the negative binomial exponent, but for the larger samples, k was low, indicating overdispersion (Figs. 3–5; Table III). The 3 populations all followed the same overdispersion pattern.

Table IV. Significance of differences in infestation prevalence by site and host substrate: *P*-values of Barnard's exact tests. Italics indicate differences significant at only the 10% confidence level ("suggestive" differences) and bold indicates differences significant at the more convincing 5% confidence level.

Host substrate	Algodonal vs. Chiribaya Alta	Chiribaya Alta vs. Yaral	Yaral vs. Algodonal
Scalp	1.000	*0.087*	0.365
Hair	0.617	**0.039**	**0.020**
Scalp or Hair	1.000	*0.087*	*0.100*

Prevalence was predominantly affected by location (environment), not site-level status or cultural affiliation (Tables V, VI). When we compare prevalence in each of the 3 populations with one other, the inland site (Yaral) has significantly or suggestively lower prevalence than does the population from Chiribaya Alta on hair, scalp, or all host substrates combined, and significantly or suggestively lower prevalence than does the population from Algodonal on hair or all substrates combined (Tables II, IV). The research design using contrasts between the 3 sites allows us to further clearly distinguish between the roles of location (that is, environment), general socioeconomic status of the site, and cultural affiliation. When we compare prevalence in the groupings that contrast each of the 3 axes or variables, the inland site (Yaral) has significantly or suggestively lower prevalence than do the 2 coastal sites combined on hair, scalp, or all host substrates combined, but we found no remotely significant difference in site-level prevalence by socioeconomic status of the site nor by cultural affiliation (Tables V, VI). Prevalence was significantly higher in the 2 coastal valley populations than at Yaral in the middle valley, with louse infestations in coastal populations apparently about twice as common as they were inland at Yaral (Tables V, VI).

Comparing only the 2 Chiribaya populations, prevalence of louse infestations was higher at the coastal site of Chiribaya Alta than at the inland site of Yaral among adults, subadults, and in the whole populations (Tables II, IV), but this pattern was significant or suggestive only when the populations were not divided into age groups (Tables II, IV, VII, IX), presumably because the sample sizes are too small when divided into age groups. Louse prevalence was higher among males than among females at every site, but the difference was not significant within any of the mummy populations (Tables VII, VIII), nor between any of the populations (Tables VII, IX), nor by any of this study's 3 axes or variables (location, status, or cultural affiliation) (Tables X, XI). While there is a hint of a pattern of higher prevalence among men, louse infestation cannot be conclusively shown to be related to the sex of the host in these populations.

The high prevalence of lice among subadults at Algodonal compared to subadults at the 2 Chiribaya sites (Tables VII, IX, X, XI) sites was presumably due to their different cultural affiliation (Tables X, XI) since no comparable differences are found when the sites are lumped by location (environment) or site-level status (Tables X, XI). That is, some culture-specific practices or conditions among Ilo-Tumilaca/Cabuza people led their subadults—but not adults—to have a higher prevalence of louse infestations than did their Chiribaya peers. We found no significant differences between prevalence on hair, scalp, or both at any 1 site, at coastal sites lumped together, or at all 3 sites lumped together. This similarity between the prevalence on either host substrate suggests that assessments of louse prevalence may be fairly robust and not significantly affected by differences in the availability of one or the other substrate type in different populations or samples.

Table V. Prevalence of louse infestations by location, status, or culture and host substrate.

Comparing	Compared groups	Host substrate	Assessed	Infested	Prevalence
Location	Coast	Hair	95	32	0.34
		Scalp	65	24	0.37
		Scalp or hair	96	38	0.40
	Inland	Hair	22	2	0.09
		Scalp	22	4	0.18
		Scalp or hair	22	4	0.18
Status	High	Hair	63	20	0.32
		Scalp	50	19	0.38
		Scalp or hair	64	25	0.39
	Low	Hair	54	14	0.26
		Scalp	37	9	0.24
		Scalp or hair	54	17	0.31
Culture	Chiribaya	Hair	85	22	0.26
		Scalp	72	23	0.32
		Scalp or hair	86	29	0.34
	Ilo-Tumilaca/Cabuza	Hair	32	12	0.38
		Scalp	15	5	0.33
		Scalp or hair	32	13	0.41

Among mummies from Chiribaya Alta and Yaral, the number of eggs/nits on the hair shafts declined with distance from the scalp (Table II), but this difference was not statistically significant (Table VIII). These interpretations are limited because only at Yaral did all the mummies have both hair and scalp preserved. At Chiribaya Alta, about 22% of the mummies lacked scalp samples, and at Algodonal almost half lacked scalp.

The 2 coastal sites have very similar prevalence of louse infestations among the populations as a whole, with no significant difference in prevalence on scalp, hair, or overall (Tables II, IV). Neither the sites' strikingly distinct cultures nor their dramatically different socioeconomic status, as indicated by grave goods, had any perceptible effect on louse prevalence overall (although the subadults at Algodonal had higher prevalence of infestation than did the subadults at Chiribaya Alta [Tables VII. IX]). Mean intensity on hair shafts, however (Table II), was significantly higher at Algodonal (41.8) than at Chiribaya Alta (6.6), at the 5% confidence level, using Neuhauser's location test. Mean abundance at Algodonal (15.7) was higher than at Chiribaya Alta (2.1) (Table II), but the difference is not significant.

The lower prevalence and mean abundance at inland Yaral relative to coastal Chiribaya Alta and Algodonal may be due to environmental conditions directly, such as Yaral's higher elevation, warmer temperatures, or greater aridity inland from the frequent coastal fog, or indirectly as a result of cultural responses to the inland environment such as differences in farming and pastoralism practices, clothing, housing, or other behavior.

Table VI. Significance of differences in infestation prevalence by location, status, or culture and host substrate: *P*-values of Barnard's exact tests. Italics indicate differences significant at only the 10% confidence level ("suggestive" differences) and bold indicates differences significant at the more convincing 5% confidence level.

Host substrate	Coast vs. inland	High vs. low status	Chiribaya vs. Ilo-Tumilaca/Cabuza
Scalp	*0.099*	0.207	1.000
Hair	**0.017**	0.505	0.221
Scalp or Hair	*0.064*	0.412	0.489

Prevalence among subadults (including infants) at Chiribaya Alta was about 25%, significantly lower than the 50% among adults at the 5% confidence level (Tables VII, VIII). The other Chiribaya site, Yaral, had a lower prevalence overall but a comparable marked age difference, with 14% of subadults infested compared to 29% of adults (Table VII). While the difference by age at Yaral is not significant (Table VIII), the trend is the same. These findings agree with Reinhard and Buikstra (2003), who found in a smaller sample of Chiribaya mummies that children were least infested and that men were most infested. This is the reverse of modern louse epidemiology, in which children are most often infested and men are rarely infested (Mellanby, 1942; Ibarra, 1989; Mumcuoglu et al., 1990; Ibarra and Hall, 1996; Ibarra et al., 2000).

The difference in prevalence between Chiribaya adults and subadults might be related to the combination of the braided hair style worn by adult men but not by subadults, which might have promoted louse infestations among Chiribaya men, and the social setting style of children. Today, children spend time in childcare and school settings promoting louse infestation (Reinhard and Buikstra, 2003). Reinhard and Buikstra (2003) suggested that the low prevalence of infestation among Chiribaya children could indicate that they experienced social settings different from those shared by modern children. Louse infestation can be connected to close environments and overcrowding (Falagas et al., 2008), and the reduced prevalence in Chiribaya subadults suggests that they may have spent less time in crowded settings. Modern children from large families are more likely to be infested than children from small families. Childcare facilities, schools, and preschools in the modern world promote social interaction between children and increase louse infestation. The contrast in louse prevalence between the Chiribaya children and modern children highlights the importance of schools and other child-centered social activities in promoting infestation. Also, Chiribaya burials often include sturdy, tight combs that were used for grooming or "nit picking" and could have limited infestation.

In contrast to the pattern at the 2 Chiribaya sites, at the Ilo-Tumilaca/Cabuza site of Algodonal the higher prevalence of infestation was the opposite: greatest among the subadults (including infants), although unlike at Chiribaya Alta, the difference

Table VII. Prevalence of louse infestations by site and demographic variables.

Site	Demographic category	Assessed	Infested	Prevalence
Algodonal	Male	5	2	0.40
	Female	12	3	0.25
	Unknown sex adult	5	3	0.60
	Adult	22	8	0.36
	Subadult not infant	3	2	0.67
	Subadult including infant	9	5	0.56
	Infant	6	3	0.50
Chiribaya Alta	Male	13	8	0.62
	Female	19	8	0.42
	Unknown sex adult	0	0	
	Adult	32	16	0.50
	Subadult not infant			
	Subadult including infant	36	9	0.25
	Infant			
Yaral	Male	5	2	0.40
	Female	2	0	0.00
	Unknown sex adult	0	0	
	Adult	7	2	0.29
	Subadult not infant			
	Subadult including infant	14	2	0.14
	Infant			
All 3 sites	Male	23	12	0.52
	Female	33	11	0.33
	Unknown sex adult	5	3	0.60
	Adult	61	26	0.43
	Subadult not infant			
	Subadult including infant	59	16	0.27
	Infant			

between them was not significant (Tables VII, VIII). Prevalence among adults was grossly similar at all three sites, but prevalence among subadults (lumped with infants) was significantly higher at Algodonal than at Chiribaya Alta at the 5% confidence level, and higher at Algodonal than at Yaral at the suggestive 10% level. Prevalence among adults at Algodonal was about 36%, while prevalence among subadults there was about 56% (Tables VII, IX).

This higher prevalence of lice among subadults at the immigrant Ilo-Tumilaca/Cabuza village suggests that distinctive cultural practices there promoted louse infestations in children in some way. It may suggest that children spent more time in crowded settings, or that they were groomed less effectively. The higher mean infestation intensity at Algodonal (Table II) suggests less effective grooming in the Ilo-Tumilaca/Cabuza population.

Housing arrangements might have contributed to different patterns of crowding and louse infestation prevalence. Owen (2005) showed that Chiribaya villages were often composed of walled compounds containing mazes of corridors, rooms, and open spaces, while Ilo-Tumilaca/Cabuza people tended to live in smaller, free-standing houses of just one or a few rooms. The effects of these very different architectural patterns on crowding and the spread of infestations would be complexly conditioned by family size and composition and how the spaces were used, but it seems likely that they played some role.

Table VIII. Significance of differences in infestation prevalence by sex and age categories at each site, at coastal sites, and at all sites: *P*-values of Barnard's exact tests. Italics indicate differences significant at only the 10% confidence level ("suggestive" differences) and bold indicates differences significant at the more convincing 5% confidence level.

Mummies from	Male vs. female	Adult vs. subadult including infant
Algodonal	0.537	0.383
Chiribaya Alta	0.403	**0.034**
Yaral	1.000	0.452
Coastal sites	0.194	0.191
All 3 sites	0.157	*0.074*

Table IX. Significance of differences in infestation prevalence by site and demographic variables: *P*-values of Barnard's exact tests. Italics indicate differences significant at only the 10% confidence level ("suggestive" differences) and bold indicates differences significant at the more convincing 5% confidence level.

Demographic category	Algodonal vs. Chiribaya Alta	Chiribaya Alta vs. Yaral	Yaral vs. Algodonal
Male	0.494	0.494	1.000
Female	0.389	0.442	1.000
Adult	0.359	0.373	1.000
Subadult including infant	*0.077*	0.644	**0.042**

Owen (2005) also argued that the Ilo-Tumilaca/Cabuza people were refugee immigrants to the coastal valley, allowed to peacefully settle as a lower-status minority in their own separate settlements interspersed between the larger, established, prosperous Chiribaya villages. The immigrants appear to have had limited access to some resources, such as fruit trees and some shoreline shellfish gathering areas, and their burials tended to contain fewer and simpler artifacts than did most Chiribaya burials. The higher prevalence of louse infestations among their children may have been another correlate of low status in prehistory, much as it is today (Govere et al., 2003; Willems et al., 2005; Balcioglu et al., 2007).

At all 3 sites, louse prevalence was higher among males than among females, although the difference was not significant at any site or at all the sites combined (Tables VII, VIII). One interpretation of this possible trend is that some form of social distance limited interaction between men and women; another is that women may have experienced more effective self-grooming or grooming by others. Hairstyle has a known effect on louse prevalence. Longer hair (Speare and Buettner, 1999) is associated with higher intensity and prevalence of infestation. Both men and women in all 3 populations usually had long hair, but Chiribaya men were buried with elaborate hair styles that covered the scalp in tight, interwoven braids. Shielded by these hair styles, the lice might have found men to be more hospitable hosts. The men's braided hair was clean. It is likely that Chiribaya men had more lice for the same reason that modern girls are more infested than boys: long, clean hair promotes louse infestation. Rosenzweig and Artzi (2011) note that close-fitting textile hats, roughly comparable to stocking caps, were found with men more than women in Chiribaya cemeteries. Hats promote louse infestation by keeping the head humid. Aridity is a key factor that inhibits louse development.

As noted above, one Chiribaya mummy exhibited maxillary pathology consistent with pronounced mucocutaneous leishmaniasis. This mummy had the highest scalp louse infestation and had his hair shorn close to the scalp (Martinson et al., 2003:fig. 9). This hair treatment was unique among the large sample of mummies and hints at social isolation. The high egg/nit count and egg

Table X. Prevalence of louse infestations by location, status, or culture and demographic variables.

Comparing	Compared groups	Demographic category	Assessed	Infested	Prevalence
Location	Coast	Male	18	10	0.56
		Female	31	11	0.35
		Unknown sex adult	5	3	0.60
		Adult	54	24	0.44
		Subadult including infant	45	14	0.31
	Inland	Male	5	2	0.40
		Female	2	0	0.00
		Unknown sex adult	0	0	
		Adult	7	2	0.29
		Subadult including infant	14	2	0.14
Status	High	Male	13	8	0.62
		Female	19	8	0.42
		Unknown sex adult	0	0	
		Adult	32	16	0.50
		Subadult including infant	36	9	0.25
	Low	Male	10	4	0.40
		Female	14	3	0.21
		Unknown sex adult	5	3	0.60
		Adult	29	10	0.34
		Subadult including infant	23	7	0.30
Culture	Chiribaya	Male	18	10	0.56
		Female	21	8	0.38
		Unknown sex adult	0	0	
		Adult	39	18	0.46
		Subadult including infant	50	11	0.22
	Ilo-Tumilaca/Cabuza	Male	5	2	0.40
		Female	12	3	0.25
		Unknown sex adult	5	3	0.60
		Adult	22	8	0.36
		Subadult including infant	9	5	0.56

clustering are consistent with community isolation as defined archaeologically (Reesor, 2021) or neglect as defined in forensic science (Lambiase and Perotti, 2019). Reesor (2021) explains that because grooming removal of lice is a social activity performed by kin groups, when an individual with lice is removed from their social group they will inevitably see an increase in infestation. This individual is the best case we have found that profound physical pathology could have led to social isolation with resulting severe louse infestation.

We believe that this study demonstrates that archaeological parasite data can be assessed with epidemiological tools to reveal useful information about both comparative patterns of parasite infestations in conditions that no longer exist for study and social history. The research design modeled here validated the data by demonstrating overdispersion, identified ecological conditions as the primary determinants of louse infestation in contrast to social status or cultural affiliation, and revealed significant patterns in the prevalence of infestation among subadults that raise further questions about living conditions, social interactions, childrearing practices, and other possibilities. This is a propitious start for ectoparasite studies of mummy populations.

Table XI. Significance of differences in infestation prevalence by location, status, or culture and demographic variables: *P*-values of Barnard's exact tests. Bold indicates significant difference at the 5% confidence level.

Demographic category	Coast vs. inland	High vs. low status	Chiribaya vs. Ilo-Tumilaca/Cabuza
Male	0.622	0.361	0.622
Female	0.500	0.228	0.630
Adult	0.639	0.259	0.557
Subadult including infant	0.244	0.724	**0.037**

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