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ORIGINAL ARTICLE

# Head lice and body lice: shared traits invalidate assumptions about evolutionary and medical distinctions

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## Abstract

Human louse-borne diseases are reemerging overseas and biological study of their arthropod vector, *Pediculus*, is needed. In an observational study on head lice, morphological features on the surface of the human host and on closely associated personal objects, such as clothing, influenced location of lice. Given optimal conditions, head lice readily transferred to the body and clothing, fed on the 'naked' body, retreated into, and laid eggs in, clothing or body hair, from which viable nymphs hatched and in turn continued the life cycle. Both wild and colonised head lice developed and reproduced without scalp contact or hairs and withstood periodic separation from the host. Further, head lice elicited the same dermatopathological effects as are reported for body lice. The belief that only established body lice infestations are a public health threat is challenged; an alternative disease process is proposed; and further basic research into this parasite is strongly indicated.

*Key Words*: ectoparasite, transmission, vector competence, louse-borne pathogen, head lice, *Rickettsia prowasekii, Borrelia recurrentis, Bartonella (Rochalimaea) quintana*

## Introduction

Humans can be infested with two kinds of lice: *Pediculus* on the head and/or body, and *Pthirus pubis* in the pubic area. Both are blood-sucking but the status of the former is controversial. Since the late 1970s, lice found on the head versus lice found on the body have been considered either separate species (*Pediculus capitis* and *Pediculus humanus* respectively) or subspecies of *P.humanus* (Busvine 1978, 1980a, 1985, 1993; Schaefer 1978; Maunder 1983; Gratz 1985, 1997; Burgess 1995; White and Walker 1995; Amevigbe *et al* 2000). This is despite the fact that, under experimental conditions, they can interbreed and produce fertile offspring (Bacot 1917; Nuttall 1917; Buxton 1947; Busvine 1978; Maunder 1983). Different sizes of head and body lice found on the same individuals led to the conclusion of separate subspecies (Busvine 1978). Yet, there are no consistent points of distinctive morphology (Ferris 1935) and identification has depended only on location found on the human body surface (Busvine 1980a; 1993; Maunder 1983). The current view is that lice found on the human body and clothing (and close personal effects, eg bedding) have evolved specific behavioural and physiological adaptations (particularly egg laying in cloth), which are not shared by lice found living on the scalp (head lice) (Busvine 1978; 1985).

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Table 1 lists, with references, some defining behavioural and physiological traits attributed to body lice and, more importantly, their presumed exclusive vector competence. However, early last century, eradication of all human lice was advised to prevent devastating louse-borne pathogen (LBP) epidemics (Buxton 1947) - epidemic typhus, louse-borne relapsing fever (LBRF) and trench fever caused by *Rickettsia prowasekii, Borrelia recurrentis* and *Bartonella (Rochalimaea) quintana* respectively. Even though such outbreaks are associated with heavy infestations over the body and clothing (Busvine 1978; 1980b; 1985), earlier investigators did not exonerate head lice from a role in disease transmission. In particular, the potential for head lice to spread down the body in times of extreme neglect to become 'body lice' was suggested by experts (Nuttall 1917; Buxton 1947). Furthermore, head lice have been shown to transmit typhus in laboratory experiments (Murray and Torrey 1975). Yet,



it is generally denied or omitted, in modern reviews of the medical implications of *Pediculus*, that head lice could possess the traits necessary for vector competence in epidemic situations. These include the ability to cause severe dermatological conditions or to multiply in abundant numbers over the surface of the body and leave sufficient infective faeces on the human, clothing and linen, thought critical to facilitate the inoculation of LBP (Maunder 1983; Goddard 1989; Peters 1992; Burgess 1995).

In this regard, head lice have been said not to constitute a public health issue (Gratz 1985; Burgess 1995).

Yet, there is no solid study to support the exclusivity of these distinctions. Recently, an Australian genetic study has found that head and body lice are almost certainly the same species (Leo *et al* 2002) and this is supported by other investigators' work presented at an international conference on lice and louse-borne disease (Dalgleish 2002). Hence, head lice cannot be excluded as vectors on the basis of species status. Thus, it remains that the validity of separate vector potential depends very much on the reality of the claimed behavioural and physiological differences between the two forms.

**Table 1**
**Characteristics presumed to distinguish body lice from head lice and/or linked to vector competence**

| | |
|---|---|
| **Habitat site choice and related behaviour** | |
| * live on both body and clothing | (Nuttall 1917; Buxton 1947) |
| * evolved habitation of human clothing avoiding even body hair (hence 'clothing lice') | (Busvine 1978; Maunder 1983) |
| * migrate down from clothing to the skin to feed and rapid movement over the body | (Nuttall 1917; Maunder 1977; Burgess 1995) (Maunder 1983) |
| * move away from body to clothing when human exercises | (Maunder 1983) |
| * found squatting quietly in clothing after removal | (Buxton 1947) |
| * variable distribution depending on clothing texture or arrangement | (Buxton 1947) |
| * distinctive preference for attachment, or transmission, to rougher clothing | (Nuttall 1917; Buxton 1947; Maunder 1983) |
| **Oviposition site choice** | |
| * eggs variably found on body hair, clothing and bedding | (Nuttall 1917; Buxton 1947) |
| * on near naked tribes, eggs found on bead necklaces | (Busvine 1978) |
| * eggs or live lice in clothing, and excoriations on body, are sign of infestation by body lice | (Epstein and Orkin 1985; Burgess 1995) |
| * oviposit in seams of clothing close to skin | (Nuttall 1917; Buxton 1947; Maunder 1983; Burgess 1995) |
| * prefer clothing over body hair for oviposition | (Maunder 1983; Burgess 1995) |
| **Other characteristics** | |
| * long starvation times allow temporary separation from host in discarded clothing or bedding | (Busvine 1978) |
| * able to multiply to larger numbers over body, clothing and linen, increasing risk of disease transmission | (Maunder 1983) |
| * bites can cause severe skin injury, sensitisation of the host and distinctive 'vagabonds' disease' skin condition | (Buxton 1947; Maunder 1983; Goddard 1989; Burgess 1995) |
| * voluminous (blood-contaminated) faeces cause irritation and are vehicle for disease by transmission through bite wounds, conjunctiva, respiratory membranes | (Buxton 1947; Maunder 1983; Peters 1992; Burgess 1995) |
| * able to be colonised in laboratory using human volunteers or rabbits; survive on twice- or once-daily feedings | (Burgess 1995; Amevigbe *et al* 2000) |
| * larger size found of body lice collected from dual infestations | (Busvine 1978) |
| * independent population sizes of body lice versus head lice in dual infestations | (Schaefer 1978) |

Head lice, in particular, are poorly controlled and increasingly prevalent worldwide (Bailey and Prociv 2000; 2001). Coincidentally, louse-borne diseases are reemerging. In 1997, 100,000 cases of typhus occurred among refugees in Burundi, the largest outbreak since World War II. The agent of trench fever is now a confirmed cause of bacillary angiomatosis in AIDS patients and endocarditis and trench fever among body lice infested urban dwellers in the USA and Europe (Raoult 1998). There are an estimated 10,000 cases of LBRF in Ethiopia per year (Raoult and Roux 1999). In the past, these diseases killed millions and threatened humanity. Thus, the biology of this arthropod vector deserves serious study. Some key questions are:

(i) whether the head louse could disperse from the scalp and survive away from it in the first instance;
(ii) whether is it capable of acting in a body louse-like manner if given the opportunity; and
(iii) whether it can elicit severe dermatological reactions and transmit louse-borne pathogens.

The present study explored the first two of these questions and, in addition, reports observations relevant to the last question.

Early pioneers and laboratory assistants have been infected or killed handling infectious lice during louse-borne disease research (Nuttall 1917; Buxton 1947; Brouqui *et al* 1999; Raoult and Roux 1999). The basic appearance and behaviour of human lice are poorly understood; we have recently documented the life-stage sizes of local head lice during rearing experiments and explored their movements (Bailey and Prociv 2002). Behavioural information from this and the present paper have assisted with handling the first imported laboratory body-lice reference strain in Australia and interpreting subsequent resistance assays at the University of Queensland (supervisor, Dr Stephen Barker, Department of Microbiology and Parasitology). Lice themselves are used increasingly as tools in resistance, pathological and forensic investigations (Lord *et al* 1998; Brouqui *et al* 1999; Hemingway *et al* 1999; Roux and Raoult 1999; Rydkina *et al* 1999; La Scola *et al* 2001). Looking at many neglected aspects of behaviour precluded sacrificing numbers in large quantitative tests. This study provides various observations on behaviour, dispersal and rearing of lice sourced directly from the scalp. Explanatory notes will be of value to further study and to explore their vectorial potential and control.

## Materials and Methods

### Background

Nearly 1000 wild head lice (donated from the scalp of over 40 unrelated adults and children of various race within and outside Brisbane) and experimentally reared head lice were studied intermittently over two years. Collecting and acclimatising sufficient wild lice numbers prior to experiments or rearing is extremely laborious (Cole 1966; Murray and Torrey 1975). A rapid sorting method helped identify viable specimens which could otherwise be missed, or dismissed when only stunned or starving (Bailey and Prociv 2002): In addition to righting overturned lice and rinsing and drying if necessary (Burkhart and Burkhart 2001), separating and brushing lice with a cloth or hairs released them from clutching each other or debris and many revived this way. The presence of all of three vital signs - clasping the hair; crawling along it at normal speed (about 18-24 cm/min for adult lice; slower for nymphs); and resisting being shaken off - was highly predictive of true viability. For example, from 116 lice of moribund appearance upon receipt, 94% selected as above were harvested for experiments and behaved normally. The few lice remaining were confirmed the only ones unable to take a blood meal and revive, and were rejected.

The viable wild lice were kept inside nearly air-tight jars containing hairs or various cloths, in the dark in ambient conditions, or incubated at 28-31°C, relative humidity (RH) 70-80%. They were fed 20-120 min on the investigator's forearm or other areas two to three times a day. Dispersal, settlement and oviposition behaviours were explored in isolated tests and also by releasing lice unconfined during more complex host interactions: eg on clothing during natural human movement. Several potential oviposition substrates were provided.

### Dispersal, mechanical factors

Migratory behaviour both on and off the host was observed, not only of self directed movement but also in terms of host mediated mechanical factors. Unfamilar head lice behaviour reported in another study (Bailey and Prociv 2002), where lice are 'attracted' en masse to clothing or towels, for example, was further explored. Viewing with a powerful lens, dissecting microscope or macro video footage confirmed that lice could be mechanically shifted around by slight human movement. The relative ease of transfer over the surface of the human body or to other objects (including other skin or clothing) was scored by conducting several 'transfer experiments' and dividing the total number of lice shifted to an intervening object (the potential recipient surface) by the total number of lice originally placed on a focal or 'donor' object. Each test used 10-100 lice.

### Rearing head lice

From the wild, small colonies of head lice were reared against the body, using traditional methods (Nuttall



1917; Buxton 1947; Cole 1966), excepting mainly that plastic pillboxes with hinged lids were used. This allowed viewing of crucial louse behaviours and dermatological effects as they developed. Several earlier colonisation attempts identified problems (eg poor feeding through silk, gauze or synthetic netting) and enabled improved rearing conditions. First aid paper tape with light adhesive (Micropore, 3M, Canada) secured the boxes on the calf or quadriceps. The open-based boxes were either bare against the skin or had open-weave mesh (cotton voile) bases. Gently wrapped conforming bandage further protected the box against dislodgement and confined occasional escaping lice.

Colony survival was also improved by awareness of nymphal appearance (Bailey and Prociv 2002) and by carefully simulating conditions that lice living in clothing in real-life would experience: Body hair was left growing in situ or, if shaved and no mesh base present, enclosed cloth substrates were not allowed to trap the lice against the box ceiling (seams and pleats helped provide 'bridges' to the skin), nor against the plastic sidewalls with excessive debris (faeces, exuviae and sweat required weekly cleaning), but were loosely arranged to provide intermittent or near contact with the skin as the host moved, as clothing would flapping around the skin.

Wild lice were allowed long periods against the body at first to minimise loss of numbers, a phenomenon also expected during body-lice colonisation attempts (Cole 1966). After multiple offspring appeared in two weeks, host-exposure time could be reduced. Despite occasional deaths, the louse families' numbers increased, regardless of 12 hours removal during either night or day and additional intermittent removal from the host. Subsequently, the first and second generations continued to exhibit positive population growth when host contact was further reduced to only 2-3 hours every 24 hours (fed once a day), so long as feeding was undisturbed, facilitated by the host taking rest.

Between times, the lice were kept within the removed pillboxes, inverted and sealed with plastic, in incubator conditions of 31°C and 70-80% RH. Lower temperatures, found to extend head louse survival (Picollo *et al* 1998), were not used. The aim was to hatch any enclosed eggs by providing optimal conditions - as might occur if the eggs were on seams close to the skin, or if they continued to be incubated by residual warmth and humidity in unaired clothing and blankets, or in a tropical climate. Various substrates, eg pieces of shirt and bedding linen, were variably enclosed to test oviposition.

In another experiment, custom-made paper tape-sealed porous cloth pads of fine cotton were employed to hatch eggs and raise first instar nymphs against the forearm. In colder months, two thick long-sleeved shirts maintained warmth and the patches were dampened in dry weather. The patches did not require removal for weeks despite showering and submergence during swimming. The conditions simulated those experienced by body lice eggs under never removed clothing on humans exposed to moisture or rain. All experiments were carried out by the fully informed primary investigator (A.B.) on herself without financial support or direction from any business or institution. In preparation for an unconnected body-lice project (not the subject of this paper) test head lice were fed by the primary investigator (A.B.) on rabbits with animal ethics committee approval (University of Queensland) and from which results are given. Unless otherwise stated, 'lice' refers to head lice.

## Results

### Viability of head lice away from the head and retention in host surroundings

Head lice are considered reliant on many feeds daily and only from the scalp. End survival times for most lice were not recorded specifically. However, of 209 donated lice of mixed stages used in tests in ambient environmental conditions, time from donation or last laboratory feed to natural death or end of experiment ranged from 1-42 h. In another group of 61 lice fed simultaneously till repletion then starved for 15 hours in darkness at 27°C and 70% RH, 93% survived unharmed. Colonized lice survived even longer between feeds.

Near instant, and repeated, blood-feeding from the human host on areas other than the scalp was a highly predictable and successful event for wild and colonised head lice. All of 946 lice that passed the viability check and which had suffered a deprivation period took a feed from hairy body skin, relatively hairless and even glabrous skin (ie palm of hand). This also occurred in open and well lit conditions. If released on clothing, cloth pieces, intact body hair or cut hairs near the skin, head lice readily reached, or completely walked over, the edges to begin blood-feeding.

With neither scalp nor body hairs to guide them, newly emerged nymphs (regardless if hatched from cut scalp-hairs or successively reared in boxes without hair) also crawled over various surfaces to find the skin and fed normally, providing they were left undisturbed in rearing boxes or patches simulating body-lice conditions.

Successful feeding by head lice on the body was evident by distension of, and rapid movement of human blood through the gut, accompanied by repeated excretion of bloody faeces (Figure 1 photo series). Left undisturbed, lice fed and defecated continuously in one position about 5-35 min, or repeatedly in various positions for up to two hours. Unrestricted feeding generally promoted longer survival times.

## Dispersal by forced transfer

This is a most neglected, yet possibly very important, dispersal mechanism with regard to the scientist and public control of body lice infestations.

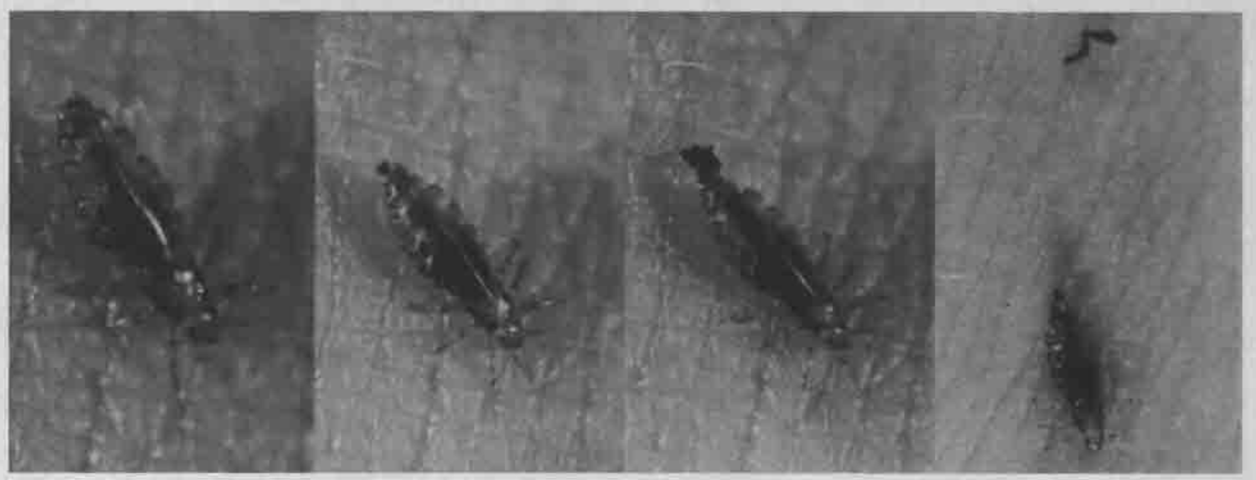

*Figure 1. Louse from scalp infestation taking blood-meal from the forearm and voiding faeces over a 35 min period. Note the louse has walked off, leaving blood-contaminated faeces at the wound site, and is still excreting faeces at a new position on the skin*

Lice removed from the scalp have been said to be weak or dying and assumed unable to persist in clothing. However, recently fed lice actively scaled skin or smooth clothing as quickly as hair shafts. Viable head lice also held fast to retentive surfaces, eg onto cotton fabric, as strongly as to hairs. This was despite violent shaking, a blast of compressed air or the negative pressure produced by a 1200 W vacuum cleaner tested at 5 cm distance from the louse. Unless on unsecured hairs or fibres or actually touched, all of 48 lice tested clung to these substrates during the above three interventions. Body lice are said to differ biologically from head lice by their retreat into clothing during human movement. However, head lice clinging to skin or exposed hairs (eg widely spaced body hairs) often moved into clothing folds or seams, regardless if fresh from the scalp or artificially reared. Of 106 lice released over the wrist, leg or abdomen, all instantly moved as a group to the inside of an overlying sleeve, sock or shirt, respectively, during disturbance. This remarkable exception to accepted beliefs invited further study and also shed light on body lice dispersal mechanisms. Perhaps because lice cling so well, there is an assumption that lice can only disperse by self-directed behaviour, eg deliberate walking from one single hair to another (Maunder 1977; Chunge *et al* 1991; Canyon *et al* 2002). Indeed, healthy head lice never dropped, even from the tips of scalp hairs while shaken or while the human walked along. However, given suitable conditions, the lice dispersed from scalp hair and over the human or environment by two basic phenomena:

(i) forced transfer; as well as

(ii) natural parasite migration over confluent surfaces.

Contrary to current thinking, viable head lice can be forcibly and quickly dispersed from a densely infested scalp during natural events, the dynamics of which have been partly explored (Bailey and Prociv 2002). For example scratched out head lice were often seen dropped to the human body or another surface. They could be flicked suddenly across long distances without static forces (Bailey and Prociv 2002; personal communication Dr J Ross, Physics Department, University of Queensland). Gravity, a sudden bump or the wind then shifted lice over smooth surfaces; otherwise they remained stranded, sometimes clutching debris. Alternatively, they were picked up on the investigator's sleeve, from where they often mobilised to seek out the skin. This illustrates some events that could disperse plentiful neglected lice in extremely unhygienic and crowded circumstances. Normally, removing head lice entirely from thick hair tresses is a challenge. Once dispersed, however, hair-like fibrous materials that humans use regularly for protection, hygiene and comfort (clothing, hats, towels, bedding) were confirmed to retain live lice or then transfer them back and forth, depending on subsequent host behaviour.

Only a few experiments were needed to recognize a trend for live lice to disperse according to human influence and the surface textures encountered. However, additional tests are listed to illustrate the mechanics (Table 2).

Examination of the results shows roughly that, if the same force were applied, the lice held fast or instantly transferred depending on the surface, with the more retentive surface keeping or taking the lice. Thus, lice



Table 2

**Forced transfer of head lice between louse-infested potential donor substrate and potential recipient substrate**

| Infested donor substrate | Potential recipient substrate | No. of strokes | % transfer |
|---|---|---|---|
| polished wood | glaborous skin (palm of hand) | 1 | 60% |
| polished wood | silk or smooth cotton shirt | 1 | 100% |
| polished wood | cut tress of hairs | 1 | 100% |
| polished wood | short-haired volunteer | 1 | 100% |
| polished wood | long-haired volunteer | 1 | 100% |
| vellous skin | glossy metal tool | 1 | 0% |
| vellous skin | vellous skin | 1 | 35% |
| vellous skin | vellous skin | 3 | 40% |
| vellous skin | smooth cotton shirt | 3 | 46% |
| vellous skin | tress of hairs | 1 | 100% |
| vellous skin | coarse linen shirt | 3 | 100% |
| vellous skin | rough cheesecloth, towel | 1 | 100% |
| vellous skin | woollen jumper, blanket | 1 | 100% |
| hairy skin (of hirsute male arm) | polished wood | 3 | 0% |
| hairy skin | smooth cotton shirt | 3 | 70% |
| hairy skin | cheesecloth, coarse hessian | 1 | 100% |
| crisp cotton bed linen | stiff implement (wood ruler) | 3 | 100%, then fell off |
| crisp cotton bed linen | stiffly held hairs | 3 | 100% |
| smooth nylon taffeta cap | stiff implement (wood ruler) | 3 | 70%, then fell off |
| smooth nylon taffeta cap | stiffly held hairs | 3 | 100% |
| smooth cotton shirt | glaborous skin (palm of hand) | 1 | 0% |
| smooth cotton shirt | vellous skin | 1 | 0% |
| smooth cotton shirt | vellous skin | 3 | 30% |
| smooth cotton shirt | smooth cotton shirt | 3 | 46% |
| loosely suspended 2000 hair tress | regular comb | 1 | 0% |
| loosely suspended 20 hair tress | vellous skin | 3 | 0% |
| loosely suspended 20 hair tress | loosely suspended hair | 1 | 0% |
| loosely suspended 20 hair tress | loosely suspended hair | 3 | 7% |
| loosely suspended 20 hair tress | towel | 1 | 0% |
| loosely suspended 20 hair tress | towel | 3 | 6% |
| 20 hair tress firm against board | stiffly held hairs | 3 | 40% |
| 20 hair tress firm against board | volunteer's own hair leant over | 1 | 37% |
| 20 hair tress firm against board | smooth cotton shirt | 3 | 30% |
| 20 hair tress firm against board | towel | 1 | 20% |
| 20 hair tress firm against board | towel | 3 | 100% |
| 20 hair tress leant on and drawn away from | coarse hessian covered couch | 1 | 40% |
| towel, blanket, fuzzy wool | vellous skin | 3 | 0% |
| towel | stiffly held hairs | 3 | 2% |
| towel | stiffly held hairs | 11 | 100% |

crawling on the bare forearm, shoulder or a smooth benchtop are easily picked up by one gentle dab of hairs or clothing. Many hairs or rough fibres were seen to catch lice in a net-like action.

The relative movement, not the individual direction of focal or recipient objects, influenced the resultant force. A stationary rough sofa can also 'catch' lice if they are wandering on outer hairs pulled away under pressure of the body. A resistant force is necessary. Even if exposed on a few swinging hairs, lice are not necessarily grabbed by a very retentive towel. However, a firm board (simulating the hard skull) provided a sturdy resistant backing by which a levering or resultant shearing action occurred.

Lice in abundant numbers can thus transfer from an exposed position on one hair tress or piece of clothing to another in an instant, depending on the human interaction. Repeating or intensifying the motion increases the likelihood of dislodgement. This transfer occurs regardless of the 'will' of the louse as, seen under magnification, it bodily resists till more forcibly dislodged (Bailey and Prociv 2002).

Head lice tightly attached to clothing, towels or blankets and 'rejected' intact scalp hairs brushed in even direct contact, thus missing their natural 'track' or 'life-line' back to the human host, unless the cloth was reunited with the host. Their anatomical retention as well as natural clinging helps explain this (Bailey and Prociv 2002). The findings negate assumptions of exclusive biology in this regard and also suggest body lice dispersal is complex.

The dynamics at work during common host actions may influence final habitat position, as was evident in rearing boxes containing leg hair and cloth when opened during various host behaviours. Unless hanging onto thick leg hairs in situ or feeding with proboscis firmly embedded, the head lice were netted by their cloth home during slightest host movements. As leg hair was not dense, routine exercise caused all remaining lice, including newly-introduced wild lice or newly-hatched lice, to constantly shift to the jostling cloth.

## Dispersal by natural migration

Without any external forces, head lice themselves moved in a manner and direction more or less according to the structure of surfaces that guided them. If not near the scalp or retreated in other recesses (eg hair knots), they kept exploring —their movements seamless from hair to other objects as long as the next surface is surmountable and the hair not shaking.

Head lice scattered quickly from untangled cut hairs onto underlying textured surfaces including skin, paper, flannel, brushed cotton shirt, a cap and a smooth cotton pillowcase. In two separate tests, within five minutes all of 61 lice moved down from loose straight hairs laid flat on rough paper or on a cotton pillowcase. Several minutes later, most had reached the edges of the paper or pillowcase.

During unconfined release on the body when the investigator kept still, well-fed lice scattered far over the body or limbs, meeting other lice, fluidly crossing adjoining clothing and skin, and settled into thick body hair or darker folds of clothing when observed in well-lit conditions.

Lice are known to be active when conditions are still and dark during host rest (Nuttall 1917). Therefore, the potential exists for head lice wandering on outer hair - a not unknown location (Burgess 1995; Bailey and Prociv 2000) - to migrate along, or close to, the body in real-life during host rest. The following simulation experiment showed this to be possible.

Of 48 hungry lice deliberately placed into the end of a cordoned-off section of long hair left quietly resting on the shoulder of a previously non-infested volunteer, within five minutes 15 lice had crawled into contact with the shoulder skin, upon which 13 lice began blood-feeding. At 10 min from release, 13 lice had continued onto the body: 5 to the back, under the volunteer's singlet; 7 on the chest; and one had slipped off the upper arm onto the white paper-lined floor below.

Inconsistent dispersal by body lice over variously textured cloths remains unexplained (Buxton 1947). An innate or conditioned behaviour apparently causes head lice to purposely 'track' along a hair in search of the host; all of 28 lice individually placed on a loose hair climbed onto the investigator's fingernail in direct contact with the end of the hair. However, even though mature head lice speedily climbed up hairs or over smooth cloth to reach host skin at the edge, they meandered on other materials. This was possibly explained by an unmodifiable adaptation to hair.

Left on a curtain netting with discreet mesh threads separated by 1mm square holes, all of 28 lice tracked along and turned right angles at random at the cross-junctions (up to 360°), gaining little displacement in any one direction. The grid-shaped cloth forced the lice to follow an unnatural template and appear attracted to exploring the cloth. Head lice placed over a particular silk shirt held on a hanger followed the prominent vertical grain of the cloth upwards to the collar. Notably, when the shirt was laid with its grain horizontally across the chest of the investigator, the lice only travelled from left to right or vice versa.



*Figure 2a*

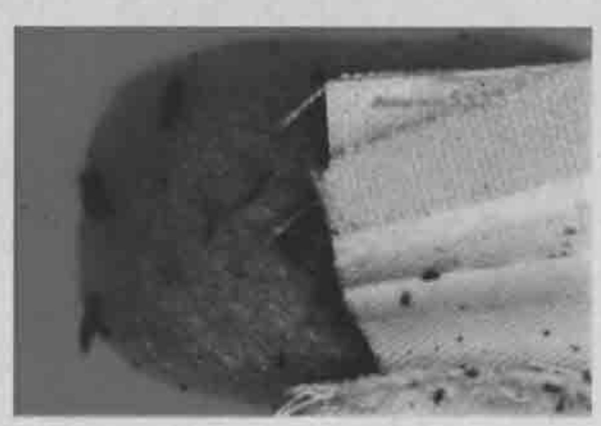

*Figure 2b*

**Figures 2a and 2b.** *Pillbox with eggs laid by head lice on cloth and some head lice present on cloth. Eggs are attached firmly to both the smooth surfaces and seams of cloth. (A few eggs can also be seen on the leg hairs); photo a few seconds later, the same lice have moved from cloth down to skin to feed during quiet tim*

Their own self-directed locomotion nevertheless equipped head lice, released on the wrist, to relocate to the body despite repeated displacement by an overlying shirt sleeve. When the investigator rested and the fabric settled down onto the wrist, the hungry lice returned to the skin. Some dismounted completely if they could bridge the gap. Others raced to a fold of fabric near the skin and fed proboscis down while most or all their legs were still clinging to the fabric. In rearing boxes, the head lice clinging to tumbling cloth were clearly seen and felt to quickly migrate down and feed on the skin during still times. Afterwards, they walked around, fed repeatedly or returned to their cloth. Again, this belies the crucial belief that head lice only survive on scalp hair and that migration from clothing down to the skin is an exclusive adaptive behaviour. The combined results suggest, rather, that lice in clothing near hairless skin carry out a misplaced normal behaviour to move in and out of hair between feeds.

**Figure 3.** *Eggs laid by head lice on leg hairs hatched on the body under continuous cover (empty hatched eggs present in photo; the newly hatched nymphs have been removed and incubated between feeds)*

## Habitat, oviposition and extended parasitosis on host

Head lice laid eggs on cloth, body hairs and other substrates (Figures 2, 3). The least tended donated head lice (fed 20 min thrice daily and otherwise kept in jars) survived for more than a week. Despite these unnatural conditions, oviposition occurred both on hairs and clothing pieces inside the jars and on the forearm hair during feeding, although infrequently.

Further experimentation confirmed that mechanical access to the skin, a nearby substrate (hair or other fibrous object), and minimal undisturbed feeding periods, were conducive to survival, mating and oviposition by head lice. This was seen when peering into rearing boxes. If the investigator exercised frequently, the flapping cloth or enclosed substrate constantly shifted lice from the skin. Most starved and thus no eggs were laid, regardless of substrates (even cut scalp hair) provided. This was thus a potential major confounder of oviposition comparisons. Keeping the host activity and exposure the same and only varying the substrates showed that, in some situations, head lice lay viable eggs on clothing and bedding linen pieces at equal or greater rates than on leg hair or cut scalp hairs inside boxes (see Tables 3, 4). Notably, head lice also laid eggs on synthetic threads, on bead necklace pieces, etc (Table 3; Figures 4, 5).

Eggs laid on various substrates were 'scatter-basketed' into different incubation situations (eg loose eggs ripped from cloth threads put in jars in incubator; eggs on leg-hairs protected by continuous wearing of boxes; eggs on forearm protected by a cloth patch; eggs on a cloth home kept with parent lice during intermittent feeding and lengthy artificial incubation). Most or all eggs hatched viable nymphs in about 9 days whether incubated against the body or isolated in suitable climatic conditions. However, the newly emerged nymphs required a timely first feed (adequate, undisturbed contact with the host skin within about 12 hours). Then, experimentally reared generations readily fed, grew and moulted regardless of substrate laid upon and in normal time frames as those observed for wild lice direct from the scalp. It was expected that large vigorous colonies could have been raised indefinitely if not terminated due to escalating sensitivity.

**Table 3**
**Oviposition by well-fed mature head lice (7 females, 3 males) accustomed to pillbox rearing on various substrates (substrates tested individually and no body hair available unless otherwise indicated)**

| Substrate tested | Oviposition rate (apportioned equally to each female) |
|---|---|
| cotton shirt or bedding linen piece | about 5 eggs/female/day |
| beaded necklace pieces, smooth blanket or towel | fewer than 2 eggs/female/day |
| synthetic wig hairs or cut pieces of cotton thread | fewer than 2 eggs/female/day |
| 1 cm pieces scalp hair first loose within box | about 2 eggs/female/day |
| 1 cm pieces scalp hair after matted to each other | about 5 eggs/female/day |
| fine fibred cloths, eg velvet | fewer than 1 egg/female/day |
| fine vellous hairs in situ | rare, attachment poor |
| unshaven coarse body hair in situ | about 5 eggs/female/day |
| fishing line, pieces of glossy plastic | 0, but occasional eggs seen on box wall |

**Table 4**
**For box containing 20 lice (of the mature lice: 10 females, 2 males) with both leg hairs and shirt cloth included, worn overnight (7 h only), incubated during day**

| | Total eggs laid on body hairs | Total eggs laid on cloth |
|---|---|---|
| during first night | 3 | 33 |
| during second night | 13 | 19 |



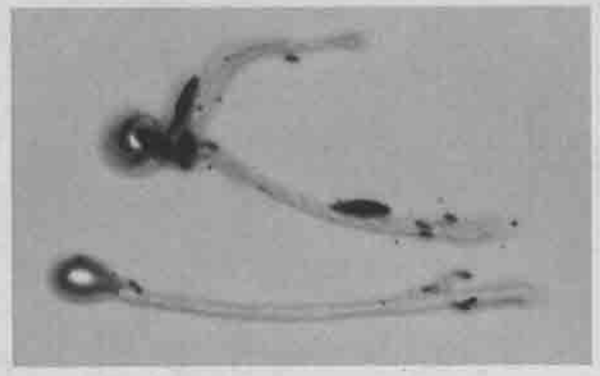

*Figure 4. Head lice eggs laid on beaded necklace piece (this challenges assumption that lice found in the past on necklaces were body lice)*

*Figure 5. Head lice eggs on purple synthetic thread and frayed edges of cloth (synthetic fibres are a relatively recent invention, thus contradicting an exclusive adaptation evolved with the appearance of clothing on humans)*

That head lice would remain in contact with the body or clothing and lay viable eggs if displaced naturally from the scalp in a less confined manner was confirmed by grooming 3 adult males and 23 adult females from scalp hair, dropping them onto, and letting them roam over, the bare forearm held still for two hours in late evening. These lice repeatedly fed, wandered (some up to the underarm and some down the hand) and laid 7 eggs (on the fine vellous arm hair) in total. As these could be easily knocked off, it could be seen that, without the protection of unchanged clothing or thick body hair, most lice and eggs would have been lost.

In another observation, the completely louse-free investigator wore 'long johns' and, over these, usual winter day or night wear. In the morning, 27 hungry, wild head lice were released on the calf of the left leg under the long johns. The investigator moved little and avoided scratching, despite intermittent bites and crawling sensations. When the long johns were removed 12 hours later, 25 of the 27 lice were found attached inside the long johns (roughly distributed, some in small groups, between ankle and upper thigh areas). The long johns were put back on and slept in overnight. At 24 hours from start, 23 live lice were found crouching again on the inside fabric of the long johns, along with 11 viable eggs attached near ankle area, leg, and seam of waistband. One egg, which later rubbed off, was attached to the investigator's sparse leg hair. Bite lesions were evident corresponding to where the head lice had travelled or congregated.

Other observations support the non-exclusivity of substrates for head and body lice. Head lice sent by unconnected members of the public were found to have oviposited eggs on cloth pieces used in transport. On the other hand, the branch of colonised body lice imported by the Microbiology and Parasitology Department, which began from wild body lice, though reared for decades on cloth and otherwise only exposed to the shaved abdomen of rabbits for feeding, lay eggs prolifically on bundles of scalp hair. In plain view of those assisting with this project (including the investigator of this study), this is the way developing lice and their eggs were successfully transported. The body lice also easily brushed up, crawled along and retreated into cut scalp hairs, and climbed up clothing pieces, as do head lice.

## Colonisation on rabbits

A separate biology of body lice is also based on the belief that they only, not head lice, can be colonized on laboratory animals. Head lice survived days longer without any human blood when fed regularly on rabbits. Of 57 starving lice, 20 lice were still alive after three days of 8 hourly feeding of 1-2h and, despite reduction to twice daily feeds, the last two lice survived till day 5. Meanwhile, 28 eggs had been laid —some loosely on the shaved rabbit abdomen during feeding and others on scalp hair or cloth while incubated —of which 14% (4/28) hatched viable, active lice. This is not dissimilar to early experimentation with body lice that eventually produced the rare laboratory ('Orlando') strain, from which only a few branches have been maintained as mentioned above (Davis and Hansens 1945; Culpepper 1948; Cole 1966).

## Clinical observations

A senile, sedentary elderly woman, admitted to a local hospital following minor hip fracture and with poorly controlled head lice and active lice throughout her clothing, had maculopapular lesions, purpuric and bloody crusts and scratch prurigo scars on scaly skin that did not vary in character over the scalp, across the hairline, down the neck and entire body. All appropriate medical and pathological investigations (eg for scabies, systemic causes) were conducted, including checking the patient's home for other parasites. The otherwise unexplained dermatosis only resolved with head-shaving of her extremely bulky hair, concomitant with the final disappearance of wandering lice that had reappeared daily over her entire body, clothing and hospital bedding and furnishings, despite changes of these. Body lice infestations are determined by a presence of eggs or lice in the clothing along with typical dermatological signs (Table 1; Figure 6); careful examination showed this 'body lice' infestation to have originated from severely neglected head lice during her immobilisation. Lice were also found living under a man's plaster cast after removal from his healed broken arm in another local hospital. Both infestations were confirmed by microscopic examination.

***Figure 6.** Healing vertical excoriations on leg of patient previously heavily infested with head lice*

The dermatological reactions experienced by the investigator after 2 years of intermittent exposure to multiple head lice bites and escalating sensitisation followed a predictable pattern (and occurred irrespective of avoiding scratching or removal of the lice after biting) and were as follows:

- end of week one: induration, intensely pruritic papules, weeping vesicles, crusts;
- end of week two: purpuric and bloody crusts and macules;
- end of week three: purpuric macules;
- end of week four: brown scaly macules;
- end of week five: faint brown and slightly scaly skin blemishes.

## Discussion

Comprehensive efforts to eliminate human blood sucking lice (head and body lice, crab lice) provided the basis for controlling the spread of epidemic typhus, relapsing fever and trench fever through much of last century (Nuttall 1917; Buxton 1947). The markedly disparate views on the exclusive biology and public health roles of head and body lice are relatively recent, of the last three decades. Early last century, Nuttall (1917) made extensive investigations and reaffirmed them to be one species. Buxton (1947) reviewed morphometric studies, considered that head lice could migrate down the body and also advised the elimination of both.

In 1978, Busvine stated that the earlier clinical definition of some insect vectors by physicians might have been too broad and suggested that head lice were of limited public health importance due to behavioural and other differences compared with body lice. On the basis of specimens collected from some individuals with dual infestations, it was concluded that independent population densities (Schaefer 1978) and a relatively larger size of body lice were evidence for a bio-ecologically separate species (Busvine 1978). These were believed consistent with an alleged recently evolved adaptation - the ability to withstand long starvation periods, habitate and oviposit in clothing worn in association with the human host (Busvine 1978; 1985).

Nevertheless, because of size overlap, it was conceded that body lice and head lice could not be reliably told apart. Busvine (1985) suggested that behavioural study, involving the unconfined release of lice on the human volunteer, was needed. Maunder (1983) questioned the bio-geographic isolation of head and body lice, but nevertheless agreed on the distinction in biology and public health importance and further stated that body lice rejected even body hair: "The major distinctive characteristic of clothing lice [as he called them] is a behavioural one; they prefer to lay their eggs attached to cloth". Direct data for this could not be found.

We attempted to redress the paucity of comparative data on head lice. In this study, isolated tests, rearing of head lice and observations on their unconfined release on the body revealed that head lice can behave in the same way as body lice. In fact, the only characteristics presumed to distinguish body lice from head lice (Table 1) that were not found to be shared by head lice were the different populations and sizes found in dual infestations, which could not be confirmed or denied, and which might be explained by different ecological constraints on various parts of the body. The range of observations invite discussion on basic louse biology as it relates to LBP epidemiology, which needs investigation (Gratz 1997).

Head lice collected from the wild have been temporarily maintained by feeding against the body prior to laboratory resistance testing (Hemingway *et al* 1999). However, there are claims that only proximity to the scalp ensures survival; displaced head lice are considered injured by host removal, dying if they voluntarily desert the scalp-hair (Maunder 1977; 1998) or overly reliant on frequent feeding (Busvine 1978). These have reinforced the belief that in the real world head lice are effectively non-viable beyond the scalp (Burgess 1995). Therefore, despite unresolved identification, lice found living on the body have been assumed to have completely separate biology to head lice (Amevigbe *et al* 2000). In this study, head lice were found capable of lengthy unfed survival times (consistent with other reports (Chunge *et al* 1991; Picollo *et al* 1998; Pollack *et al* 1999)) and extended survival after feeding on any part of the body, and were quickly conditioned and selected to lengthier starvation times (down to once-daily feeds corresponding to experimental body-lice colonies (Cole 1966; Burgess 1995)). Together these results indicate the potential for head lice to survive against the body in real life.

Healthy head lice were found to attach, retreat and oviposit in clothing, and the life cycle can continue with only intermittent association with the body and in the absence of scalp- or even body-hair. While it is conceded that head lice look like body lice, have bred with body lice and have laid eggs on cloth in older experiments (Nuttall 1917; Buxton 1947), it is nevertheless assumed that movements of lice over the human body and surrounding surfaces are unique characteristics of a body lice species or sub-species. The knowledge that head lice deftly scale hair and cling tightly during disturbance (also observed here), may underlie the assumption that healthy head lice will never move from hair except to walk to another head, and that dispersal dynamics exist mainly in terms of parasite-mediated behaviour (Maunder 1977, 1983, 1998; Chunge *et al* 1991; Canyon *et al* 2002). However, head lice were found to have the potential in the first instance to spread from scalp to body by natural migration (parasite-mediated) or mechanical forces (host-mediated).

It was established by this study that lice have morphology and behaviour that influence their natural migration, and which also cause them to be forcibly 'caught' or transferred over hair, skin and similar surfaces accordingly. The design of a grooming tool (eg comb) is an important determinant in whether or not tenacious lice are plucked from hair (Bailey and Prociv 2002). Similarly, the surface design of objects closely associated with humans, eg clothing fibres, comparable with hair or skin in offering a foothold, can shear lice away from a focal object (including the host), or protect them and provide a track for migration to and from the skin. Head lice in rearing boxes were seen to retreat by self-directed behaviour into clothing folds, stay on surfaces nearest the skin, and oviposit on seams - as do body lice. They were also instantly relocated to clothing (during host movement) while migrating, or feeding, on the skin, even if clinging to available body hair. Thus, the characteristic finding of live lice in bedding and repeated shift into clothing, after pulling off clothes or during exercise (Buxton 1947), cannot surely infer adaptation to living in clothing by an exclusive body lice species or form.

Similarly, the finding of eggs in clothing cannot be taken to indicate a preference or adaptation for clothing fibres as a substrate choice, even over body hair (Maunder 1983); otherwise, on the basis of both rearing and unconfined release observations from the present study, head lice could also be deemed adapted to clothing. Given a binary choice inside boxes, some eggs were eventually clustered in rows on hairs while other hairs were left alone, so limitation of hairs available was not a reason for more eggs laid by head lice on cloth. Yet, on the basis of Bacot's study in 1917 comparing head and body lice egg-laying rates and alignment inside boxes (which Maunder 1983, may have been alluding to), there is an inference that body lice differ from head lice in that they do not lay as often or as expertly on hairs (Bacot 1917). However, head lice here also rarely laid eggs on body hair if disturbed by clothing, or on enclosed cut hairs if not of optimum diameter or until crossed and matted together. Moreover, feeding influenced oviposition. Indeed Nuttall (1917), who conducted comprehensive experiments comparing substrates, concluded that feeding opportunity, and substrate quality and positioning, could flaw comparisons of oviposition rates and alignment. When kept the same, body lice actually laid more eggs on hair than on cloth (Nuttall 1917). Thus, oviposition by lice in clothing may largely be misplaced actions due to constant displacement and no hairy alternative nearby, the result of unmodifiable hair-adapted behaviour of *Pediculus* in general.

Preliminary genetic investigations suggest head and body lice are indeed conspecific with more genetic similarity overall than when comparing head only specimens or body only specimens sourced from different countries (Leo *et al* 2002). Even so, there is unresolved discussion on the changing forms of reared head lice or hybrids (Busvine 1978; Maunder 1983) and it could be argued that head lice may have to undergo changes through successive generations, against the body, before they can act as a vector of LBP. However, wild head lice immediately lived, reproduced and caused dermal injury in rearing containers against the body without hair. This also occurred when roaming naturally over the body, with or without clothing cover.

This study does not refute the clinical presentation of lice infestations (pediculosis corporis, pediculosis capitis) or variation in morphology. However, it challenges the assumption that bodily infestations are proof of a form with exclusive behaviour and physiology not possessed by head lice. It has, nevertheless, been argued that even if head lice demonstrate these characteristics, that they are anyway homeward-bound and remain on the scalp (and thus presumed unsuitable as vectors). This was implied, based on some tests where several released head lice did not establish in clothing and a few were eventually found in the scalp hair (Busvine 1978; 1985). Dispersal observations here suggest mechanical factors could influence such test results. As examples, head lice here merely climbed the vertical grain of a silk shirt upwards, and on the other hand, were easily knocked off crisp cotton linen or attached tightly to a woollen jumper. Body lice also climb hairs (Nuttall 1917) and variably attach and travel in clothing (23 cm/min or meander inexplicably) (Buxton 1947). A small number of released lice may scatter and are unlikely to form a colony. Buxton (1947) also reported, while collecting body lice from many people, that a few lice caught on his clothing was not a risk for establishing an infestation.

If head lice might seed bodily infestations or carry LBP, why then are not children in developed countries, in whom head lice are common, developing body lice and LBP infections? Firstly, the foci of these diseases were largely eradicated by earlier control. Secondly, body lice and LBP epidemics develop when humans live in crowded and squalid conditions where manual delousing and /or washing or weekly change of clothing are not even conducted. Travel introduction of LBP foci is a concern but a breakdown in health also allows recrudescence of Brills-Zinsser disease, whereby people carrying typhus *Rickettsia* in their blood may, if again infested with lice, seed a typhus epidemic in crowded conditions. This study's findings suggest that mechanical host-parasite interactions, rather than an exclusive parasite adaptation, are critical in the settlement, or not, of lice. Human morphology (such as hairy cover) and actions (such as clothing changes or movement, manual picking) as they relate to *Pediculus* morphology influence settlement over distinct areas of the body.

While isolated scalp infestations are usual in developed countries, during times of extremely poor hygiene 100 years ago, clinical observations showed that severely neglected head lice dispersed down the body (Nuttall 1917). In adequate living conditions, reduced intelligence or lack of custom to manually delouse are also associated with body lice (Buxton 1947; Tesfayohannes 1989). It is notable that where head lice are widely prevalent and living conditions extremely deprived, body lice infestations and LBP outbreaks also appear. In Ethiopia, the worst surge of LBRF[2] in school-aged children occurred after commencement of school (Borgnolo *et al* 1993), a well-known reservoir for head lice transmission (Bailey and Prociv 2001). In Egypt, of institutionalised orphans, only those with head lice (64%) had body lice (54%) despite the crowded conditions that facilitated transmission of the head lice (Morsy *et al* 2000). In 304 Ethiopian refugees (where nearly 100% of the children examined had head lice) the community suffered with 65% head lice overall when body lice (39%) were found to be a substantial threat (Mumcuoglu *et al* 1993).

Review of accumulated knowledge, together with the findings here, not only cast doubt on the current taxonomy but also the presumed disease process. Generally accepted transmission routes, ie, exclusive head-to-head (Speare and Buettner 2000) and body-to-body transmissions (Hatsushika *et al* 2000), are not contradicted. Indeed, the biomechanical findings support recent conclusions about the high risk for direct head-to-head transmission that existing scalp infestations present among congregating children (Speare and Buettner 2000; Bailey and Prociv 2001). Light contact would explain louse-free acquaintances of infested families, while the vigorous head rubbing children share with each other indiscriminately would generate shearing actions to transfer lice instantly (Bailey and Prociv 2001). However, regardless of site of initial attachment, other dispersal and settlement processes may occur, eg uncontrolled lice from scalp to body of the same host, as suggested by this study. In general, a primary focal population of lice, established in more readily colonised (eg suitably hairy) parts of the body, will remain isolated while clothes are regularly removed. However, lice could



then spread over the entire body, clothing, bedding and other furnishings (Nuttall 1917; Buxton 1947; Linardi *et al* 1998) if the host's living conditions deteriorate, resulting in the distinctive secondary lesions on hairless parts of the body also.

Currently, there are scant data and acknowledgment of the dermatological effects of head lice, believed only capable of causing minor symptoms (Goddard 1989; Pollack *et al* 2000). However, serious skin breakdown has been reported in past experiments (Nuttall 1917) and in neglected scalp infestations (Burgess 1995), and recent histological investigation revealed deep dermal inflammation and injury with vascular and spongiotic changes as a result of head lice bites (Bailey and Prociv 2000). The purpuric crusts resolving to brown patches seen in the case described in this study and on the investigator fit the description of vagabonds' disease. The investigator's personal experience agrees with older reports (Nuttall 1917; Buxton 1947) that the lesions worsen with escalating sensitivity of the host to repeated exposure to bites from many lice. In this study, the largest purpuric lesions developed where grouped bites caused vesicular eruptions that coalesced to form punched-out weeping sores, even without scratching. Thus, unexplained reports of variable maculopapular rash on the neck, shoulders and trunk (Epstein and Orkin 1985) accompanying severe head lice infestations are plausibly the urticated bite lesions of pioneer lice moving beyond the scalp.

Body lice are also believed to facilitate the rapid transmission of LBP by spreading blood-contaminated faeces over the surface of the host, including the clothing and bedding. However, head lice also produce voluminous blood-contaminated faeces and animal studies have shown that head lice can readily transmit typhus by biting hosts and excreting highly infectious faeces (Murray and Torrey 1975).

Head lice infestation has been increasing in prevalence, especially in schoolchildren over the last three decades, and affects millions of people worldwide (Amevigbe *et al* 2000; Bailey and Prociv 2001). The development of resistance, unreliable treatments and low-level control measures have allowed unfettered transmission of head lice through children and their families (Bailey and Prociv 2001). Body lice infestations and LBP infections are reemerging in urban settings, as well as in poorly-developed countries (Bise and Coninx 1997; Linardi *et al* 1998; Brouqui *et al* 999; Niang *et al* 1999; Raoult and Roux 1999). Elimination of lice in the individual is achievable. Until the biology of the two forms is clarified, the WHO strategy (Gratz 1985, 1997) of placing less priority on eradication of scalp infestations while emphasising global control of body lice infestations, and at the same time acknowledging the potential of LBP outbreaks, is incongruous. This study concludes that, if residual lice were allowed to harbour in scalp or body hairs by virtue of ineffective pediculicides or incomplete physical methods and if normal living conditions were to severely deteriorate, the preexisting lice have the potential to multiply and disperse over the body and between hosts and the environment. This would be a potentially dangerous situation if concomitant louse-borne disease were to recrudesce in susceptible populations.

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