

An Experimental Test of the Site Specificity of Preening to Control Lice in Feral Pigeons

Lajos Rózsa, Department of Parasitology & Zoology, University of Veterinary Science, H-1400 Budapest, P.O. Box 2, Hungary

ABSTRACT: Site specificities of ectoparasites on the host may have evolved due to the selective pressure exerted by host grooming. The present study demonstrates that the efficiency of avian preening varies among sites on the host. The study relies on the simple idea that the effectiveness of preening behavior to control lice can be quantified by the removal rate of dead lice glued onto the feathers of living birds. Two treatments were done to document site-specific differences in the efficiency of preening for louse control. The first treatment showed that lice disappear from the underwing covert feathers significantly more than from the tail feathers. A second treatment showed that preening was responsible for the differential removal of lice. There seems to be some correspondence in the site specificity of the louse species *Columbicola columbae* and that of the efficiency of preening by the host, which is the feral pigeon (*Columba livia*).

The plumage of birds is inhabited by a diverse ectoparasite fauna. Birds exhibit different behaviors to reduce their ectoparasite burden, e.g., preening plays a major role in reducing the number of chewing lice (Phthiraptera: Insecta) (Clayton, 1991). Whereas members of the suborder Amblycera tend to move on the skin and may feed partially on blood, members of the suborder Ischnocera live on the feathers, tend to feed on nonliving tissues, and may cause considerable damage to the plumage (Clayton, 1990). Birds remove lice with the bill when preening. Individuals with naturally or experimentally deformed bills have high burdens of lice (see Clayton [1991] for a review).

Ectoparasites living on different anatomical sites are attacked by different forms of grooming; the head of a bird is scratched with the feet, whereas the rest of the body is preened by the bill (Clayton and Cotgreave, 1993). The resource tracking hypothesis published by Kethley and Johnston (1975) suggests that the site specificity of ectoparasites evolved partly due to the selective pressure exerted by host preening and grooming. Ectoparasites, especially ischnoceran lice of birds, are adapted to utilize the topographical refugia in the plumage to evade preening. Clayton (1991) suggested that this idea could be tested by comparing the regional efficiency of grooming.

Here I describe the first experimental documentation of site-specific differences in the efficiency of preening for louse control. The experiment tests for regional differences in preening efficiency by comparing the removal rates of dead lice glued to different plumage regions of living birds.

Feral pigeons (*Columba livia*) were chosen for study because they are easy to collect and care for in captivity. The parasite in this study was the louse *Columbicola columbae* Linnaeus, a common ischnoceran louse on pigeons.

The sites involved in the present study were chosen on the basis of preliminary observations on the site specificity of pigeon lice. The imago (adult) lice were observed to attach to the undersurface of the rectrices (tail feathers) of pigeons. The anatomy of the imago pigeon louse topographically fits into the rough surface texture of these feathers so that the lice can insert between the barbs and thus remove themselves from the surface. These lice are not strictly specific to this site; they cannot feed or breed on the vane of the rectrices. However, a proportion of the actual burden typically is found hiding motionless on these feathers (6-20% of all imagoes in the study of Nelson and Murray [1971]). On the other hand, the eggs of the lice are usually attached to the underwing coverts (Nelson and Murray, 1971). The surface of these feathers is rather smooth and so they do not offer a topographical refugium in which to hide. On the contrary, the eggs are small enough to fit into the texture of these feathers. On the basis of these observations, it is believed that laying eggs may be a dangerous task for female lice, assuming it increases their exposure to preening. To test this hypothesis, I compared the rate of removal of imago lice from these 2 locations, i.e., the undersurface of the underwing coverts and the undersurface of the rectrices. Nymphs were excluded from the study because they have a different size and tend to be less site specific (Nelson and Murray, 1971).

A colony of feral pigeons was captured on a roof and moved into an aviary (4 × 4 × 2.5 m) built on the roof of the laboratory. Similar roofs often are inhabited by feral pigeons in the city, so the aviary is regarded as a seminatural site. The aviary was equipped with 20 m of wooden perch providing a comfortable distance between birds for preening and roosting. The colony consisted of 46 pigeons, 36 of which were involved in the study. Young birds (less than 3 mo old) and birds incubating eggs were excluded. All birds carried natural infestations of *C. columbae*.

Pigeons were handled to glue lice onto their plumage with a suitable household glue (a "super glue" with cyanacrylate as the active ingredient). The lice were collected by a modified Fair Island apparatus (Fowler and Cohen, 1983) 1 yr before the study and stored in alcohol. The lice were situated into a natural posture, parallel with the barbs, with their heads oriented toward the shafts (Stenram, 1956). Two sites, the undersurface of the underwing coverts and the undersurface of the tail, were used. Twelve lice were glued onto each of 36 birds, 3 on the underwing coverts on both sides and 3 on the undersurface of the second-to-outermost rectrix on both sides. There was no difference expected or experienced between the efficiency of preening on the left and that on the right side. The purpose of using both sides was to mimic an equal distribution of lice within a site. After the procedure of gluing, the birds were released back into the aviary. The removal rate of the lice glued to the feathers was recorded after 24 hr.

The treatment was repeated 1 mo later using the same birds but now with inhibited preening ability. To inhibit preening, the tip of the upper mandible was shortened by a few millimeters (Nelson and Murray, 1971). The aim of the repeated treatment was to assess the number of lice disappearing in the absence of preening (e.g., due to dislodgement).

Many of the lice glued onto the birds were completely absent after 24 hr. Others were absent only partially, e.g., the thorax and the abdomen were lost, but the head was still attached to the feather. I categorized lice as present if all of these 3 main body parts were present and categorized lice as absent if any of these was absent. The data are summarized in Table I.

The absence or presence of lice was determined by preening and dislodgement in treatment 1, and determined only by dislodgement in treatment 2. The results of the second treat-

TABLE I. The mean number (SD) of lice absent after 24 hr, of 6 lice glued onto each of 2 sites on each of 36 pigeons. In the first experiment the birds could preen themselves, whereas preening-impaired birds were used in the second one. The loss of lice in the second experiment serves as a control on lice lost in the first experiment due to efficient preening.

Site	Treatment 1	Treatment 2
Underwing coverts	4.67 (1.57)	1.63 (1.38)
Rectrices	0.47 (0.77)	0.38 (0.71)

ment demonstrate that not only preening but also the dislodgement of lice is site specific. The lice glued onto the underwing coverts are more exposed to aerodynamic effects than those glued on the rectrices. Moreover, the underwing coverts are lost more easily during the capture of the bird than the rectrices.

Though 2-factor analysis of variance (with treatment and site as the 2 factors) could be used to determine whether site specificity is a significant source of variation, the site specificity calculated by this method would involve the site specificity of dislodgement too. To eliminate this fault, the data were rearranged as shown in Table II. The numbers of lice categorized as present after the first treatment were adjusted by adding the mean values of lice lost in the second treatment. These modified values of the first treatment were regarded as the numbers of lice not removed by preening, and these values were used below to compare preening efficiency at the 2 sites.

In treatment 1, a total of 216 lice were glued onto the underwing coverts of the birds. The number of lice not affected by preening was 106.5 after 24 hr. These quantities (216 and 106.5) differ significantly (chi-square test, $\chi^2 = 55.51$, $P < 0.001$). Similarly, a total of 216 lice were glued onto the rectrices of the birds, and the number of lice not affected by preening was 212.5 after 24 hr. This latter quantity differs significantly

TABLE II. The rearrangement of data to calculate the effect of preening at the 2 sites in treatment 1. The mean number (SD) of lice present untouched after treatment 1, adding the mean of those lost because of spontaneous dislodgement in treatment 2, forms the quantities not removed by preening in treatment 1.

Site	Present after treatment 1	Dislodged during treatment 2	Not preened in treatment 1
Underwing coverts	1.33 (1.57)	1.63	2.96 (1.57)
Rectrices	5.53 (0.77)	0.38	5.91 (0.77)

from the value counted on the underwing coverts (chi-square test, $\chi^2 = 52.87$, $P < 0.001$) but not from 216 (chi-square test, $\chi^2 = 0.06$, $P > 0.7$).

These results demonstrate that preening is more efficient at removing lice from the underwing coverts than from the tail feathers. Thus, lice laying eggs on the underwing coverts may be more exposed to preening than those on the tail feathers. In fact, the undersurface of the tail feathers appears to be free from preening pressure.

There is a traditional view, dating back to Clay (1949), claiming that the site specificity of ectoparasites is a result of competition for resources among ectoparasite species coexisting on the same host. An alternative view, the resource tracking hypothesis, emphasizes the role of host defenses in the evolution of site specificity (Kethley and Johnston, 1975). The results of the present study are in accordance with the latter hypothesis in the sense that the data document regional differences in the effectiveness of preening to control lice. Moreover, there seems to be some congruence of this difference with the site specificity of the louse *C. columbae*, though the site specificity of this species is not pronounced.

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Synonymy of *Eimeria larimerensis* with *Eimeria lateralis*

Robert S. Seville and Nancy L. Stanton*, University of Wyoming Casper College Center, 125 College Drive, Casper, Wyoming 82601; and *Department of Zoology and Physiology, Box 3166, University of Wyoming, Laramie, Wyoming 82071-3166

ABSTRACT: Oocysts of *Eimeria lateralis* were isolated from feces of *Spermophilus richardsonii* and compared to published descriptions of *E. lateralis* and *Eimeria larimerensis* from other spermophiline rodent hosts. A comparison of these 2 eimerian species, combined with an examination of host specificity of spermophiline eimerians and host and parasite distributions, suggests that *E. larimerensis* is synonymous with *E. lateralis*.

Shults et al. (1990), Seville (1992), and Stanton et al. (1992) found 6 species of *Eimeria* in populations of Wyoming ground squirrels (*Spermophilus elegans*) in southeastern Wyoming and Seville and Stanton (1993) found 6 species in Richardson's ground squirrels (*Spermophilus ri-*

chardsonii) from Alberta, Canada. The only difference noted between the eimerian guilds from the 2 hosts was the presence of *Eimeria larimerensis* Vetterling (1964) in *S. elegans* and *Eimeria lateralis* Levine, Ivens, and Kruidenier (1957) in *S. richardsonii*. Due to the morphologic similarity of *E. lateralis* to *E. larimerensis* we compared descriptions, host ranges, and geographic distributions of these 2 species to assess their taxonomic independence.

One hundred fecal samples from *S. richardsonii* were collected after the methods of Seville and Stanton (1993). Oocysts were concentrated by flotation in saturated sucrose solution (specific