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Bird-Parasite Interactions

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14 Coevolution of avian grooming and ectoparasite avoidance

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Introduction

Ectoparasites severely reduce avian fitness when they occur in large numbers or when they serve as intermediate hosts for avian pathogens. In most cases, however, ectoparasites occur in small populations with little or no effect on the host. These small populations may be the result of host-parasite coevolution. If a parasite exerts selection on its host and the host exerts reciprocal selection on the parasite, repeated bouts of coevolutionary change can lead to coadaptation of host defence and parasite resistance. Although host defence can prevent the buildup of large parasite loads, energetic constraints will probably prohibit the evolution of perfect defence against parasites with coadaptations for resistance. Persistence of small loads on birds may therefore reflect a coevolutionary balance between defence and resistance.

Coevolution is not the only explanation for the persistence of small loads, however. If small loads have no effect on the host, they may persist simply because a bird has nothing to gain by removing them. Coevolution cannot be assumed to occur in a given system, but must be empirically inferred, which entails a three-step process. First, the adaptive function of presumably coevolved traits must be documented. Second, reciprocal selection on those traits must be measured. Third, the opportunity for coevolutionary response to reciprocal selection must be demonstrated. In this chapter I report the results of three experiments designed to address the first step—documentation of the adaptive functions of avian grooming and ectoparasite avoidance.

Coevolution of birds and ectoparasites: background

Adaptation. Process of evolutionary modification which results in improved survival and reproductive efficiency.

(Lincoln *et al.* 1982)

Coevolution is evolutionary change in two or more species resulting from reciprocal selection exerted by those species on one another (Janzen

1980; Thompson 1982, 1989; Futuyma and Slatkin 1983; Nitecki 1983). Persistent bouts of coevolution can lead to coadaptation of species living in close ecological association. Patterns of apparent coadaptation are widespread among competitors, mutualists, predators and prey, and hosts and parasites (*sensu* Price 1980). The reciprocity of coevolution makes it a unique process that can lead to complex evolutionary outcomes, such as the elaborate patterns of chemical coadaptation observed among plants and their herbivores (Spencer 1988).

Host-parasite interactions, which often show circumstantial evidence of coadaptation, are ideal testing grounds for coevolution because they include some of the most intimate associations known (Price 1980; Rollinson and Anderson 1985). In a comprehensive overview of the evolution of vertebrate-insect associations, Waage (1979) hypothesized 'extensive reciprocal coevolution' between vertebrates and their ectoparasites. Waage cited examples of presumed coadaptation between birds and ectoparasites, noting that the coevolution of these and other vertebrate-insect systems was unexplored relative to the expanding literature on plant-herbivore coevolution. Today, more than a decade after Waage's review, the situation remains the same; almost no research has been conducted on the coevolution of birds and their ectoparasites.

Birds are host to a variety of ectoparasites, including mites and ticks (Acarina), flies (Diptera), bugs (Hemiptera), chewing lice (Mallophaga), and fleas (Siphonaptera). Members of all five orders have the potential to severely reduce avian fitness when present in large numbers (Boyd 1951a; Moss and Camin 1970; Duffy 1983; Brown and Brown 1986; Shields and Crook 1987; Clayton 1989). However, most individual birds are host to small, relatively innocuous loads of ectoparasites (Rothschild and Clay 1952; Ash 1960; Baum 1968; Marshall 1981). These small loads appear to be kept in check by the birds themselves through a variety of defence mechanisms ranging from behavioural responses (Murray 1990) to immune reactions (Mathysse *et al.* 1974).

The most obvious defence against ectoparasites is grooming behaviour (Nelson *et al.* 1977; Waage 1979; Murray 1990). The predominant form of avian grooming is preening, which may be operationally defined as manipulation of the plumage with the bill. The other major form of grooming is foot scratching, which appears to control ectoparasites on the head and other regions inaccessible to preening (Brooke 1985). The precise grooming behaviour of birds is partly a function of morphology. For example, species with long, unwieldy bills scratch more than species with short bills, as illustrated by a significant correlation between the ratio of bill to body size, and the ratio of scratching to preening among families of neotropical birds (Clayton, in preparation).

Ectoparasites show apparent morphological and behavioural adaptations for resistance to host grooming. These include: (1) small size and flattened shape; (2) heavily sclerotized integuments; (3) spines, ctenidia, and numerous setae; (4) strong mouthparts and grasping claws; and (5) avoidance behaviour (Marshall 1981). For the purposes of this chapter, 'avoidance' refers to any morphological or behavioural trait that facilitates resistance to grooming. The microhabitat distributions of some ectoparasites also appear to reflect grooming-imposed selection (Waage 1979). This is best documented for species of 'chewing lice' (Insecta: Mallophaga), which tend to be more or less restricted to the wings, head, or abdomen of their hosts (Dubinin 1947; Clay 1949, 1957). Species on the wings are often elongate, compressed forms capable of flattening themselves against the surface of feathers, or inserting themselves between the barbs of feathers. Species on the head and neck, where they are protected from preening, are typically round-bodied, sluggish forms with no apparent adaptations for avoidance. Species on the abdomen tend to be intermediate in form and behaviour (Marshall 1981).

Observational data such as these suggest that avian grooming and ectoparasite avoidance are coadapted traits, but this is not necessarily the case. The elongate morphology and insertion behaviour of wing lice, for example, may not be adapted for the avoidance of preening, but to prevent lice from being blown off the host's feathers during flight (Stenram 1956). Moreover, traits may not be adaptive at all, but neutral with respect to fitness. As stated by Futuyama (1986, p. 283), 'Adaptation is an onerous concept, and the adaptive value of a trait should be demonstrated rather than assumed, for numerous factors other than adaptation can influence the evolution of a trait.' In short, if a trait's effect on fitness has not been measured, adaptation can be addressed only in a speculative fashion (Williams 1966; Gould and Lewontin 1979).

This chapter presents the results of a series of three experiments designed to explore the adaptive functions of host preening and ectoparasite avoidance. The goal of the first two experiments was to measure the relationship of preening behaviour to host fitness by determining: (1) the extent to which preening controls ectoparasite populations on the host (experiment I); and (2) the impact of ectoparasite populations on a probable component of host fitness (experiment II). The goal of the third experiment was to measure the relationship of avoidance behaviour to ectoparasite fitness by comparing the impact of preening on species of ectoparasites with different avoidance responses. The experimental system chosen for study was the rock dove, *Columba livia*, or feral pigeon, and two species of chewing lice: *Columbicola columbae* (Linnaeus 1758), an elongate, agile species found primarily on the wings, and

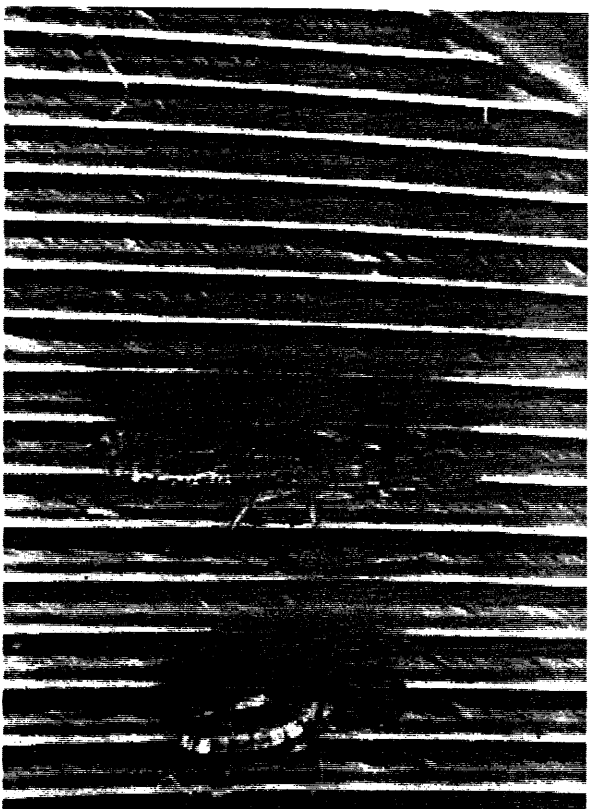


Fig. 14.1. *Columbicola columbae* (left, 2.5 mm long) and *Campanulotes bidentatus* (1.5 mm) on the vane of a flight feather. *C. columbae* uses its large posterior legs (arrows) to orient and run across the ventral surfaces of flight feathers. *C. bidentatus*, which cannot manoeuvre on flight feathers because of its small legs (not visible), is normally restricted to abdominal contour feathers. (Photo: J. Barabe.)

Campanulotes bidentatus (Burmeister 1838), a slow moving species found primarily on the abdomen (Fig. 14.1; Nelson and Murray 1971).

Rock doves and chewing lice: natural history

The rock dove was chosen for this research because it is plentiful, accessible, and adjusts well to captivity and the techniques described below. Furthermore, the composition of its parasite fauna is well known (Levi 1957; Rand 1959; Brown 1971). *C. livia* was domesticated around 4500 BC (Zeuner 1963), and introduced to North America in 1606 (Schorger 1952). North American rock doves retain considerable morphological and behavioural similarity to ancestral populations of *C. livia* in Morocco and other regions (Goodwin 1983). Although urban pigeons habituate to people, rural pigeons are as timid as other wild species of birds. The rock doves in this study were rural-trapped individuals or their offspring.

Columbicola columbae and *Campamilotes bidentatus* are members of the largest Mallophagan suborder, Ischnocera, which contains 2954 species, 2619 (88.7 per cent) of which parasitize birds; the rest are parasites of mammals (Price, Hellenhal, and Emerson, in preparation). Most species of Ischnocera are restricted to a single species or genus of host (e.g. Price and Clayton 1983; Clayton 1990a). This extreme level of host specificity makes Ischnocera an attractive group for coevolutionary analysis because specificity implies long-term association, which reduces the likelihood that current patterns of coadaptation are the result of transient past associations. *Columbicola* and *Campamilotes* are genera found only on members of Columbiformes (Keler 1939; Tendeiro 1965). *C. columbae* and *C. bidentatus* are specific to the rock dove, and are the only species of Ischnocera typically found on this host in North America (Emerson 1972). The Ischnoceran *Physconellodes zenaidurae* '... has occasionally been collected from the domestic pigeon', but its true host is the mourning dove, *Zenaidura macroura* (Emerson 1960).

Avian Ischnocera are obligate parasites that complete their entire life cycle on the host (Marshall 1981). They are dependent for reproduction on the warmth of the bird's body which they do not leave except to pass from one individual to another during periods of direct contact, e.g. between parents and offspring (except in cases of phoresy on Hippoboscid flies or other insects—see Keirans 1975). The life cycle, which requires 3 to 4 weeks, includes a nit (egg), three nymphal instars, and the adult (Martin 1934). Nits are glued to the host's feathers with a glandular cement, often in positions more or less protected from grooming, such as the gulum (throat). *C. columbae* and *C. bidentatus* are so highly specialized for locomotion on feathers that they rarely if ever venture on to the host's skin (Stenram 1956; Clayton 1990b). They also feed exclusively on the barbules of feathers (Fig. 14.2; Nelson and Murray 1971), which they metabolize with the aid of symbiotic bacteria (Eichler *et al.* 1972; Marshall 1981).

No published test exists of the direct impact of Ischnocera on host fitness. Derylo (1974a,b) reported a reduction in the egg production of leghorn chickens parasitized by Ischnocera, but the birds in Derylo's study were also host to Amblycera, a smaller suborder of Mallophaga that lives and feeds on the skin and blood of the host in addition to feathers. Amblycera are known to promote dermatitis and scratching, and are responsible for up to a 46 per cent reduction in the egg production of poultry (DeVaney 1976; Nelson *et al.* 1977). Amblycera are also known to vector avian endoparasites and pathogens (reviewed by Clayton 1990b). To date, Ischnocera are not demonstrated vectors of avian endoparasites or pathogens.



Fig. 14.2. Rock dove feather showing damage from lice. The barbules of the basal and medial regions have been consumed. The barbs and shaft are never eaten, possibly because they are too large to ingest (Clay 1950). *C. columbae* and *C. bidentatus* feed only on abdominal contour feathers. (Photo: B. Edinger.)

Experiment 1: role of host preening in louse control

Observational data and previous experiments

Birds with deformed beaks or feet often have large ectoparasite loads, apparently because of their inability to groom properly (Boyd 1951b; Rothschild and Clay 1952; Ilienko 1959; Ash 1960; Pomeroy 1962; Baum 1968; Ledger 1969; Marshall 1981). For example, I obtained a female house sparrow, *Passer domesticus*, that was missing the upper mandible of its bill, and which was host to over 1200 lice (*Briellia subtilis*) and over 400 mites (mostly *Proctophylloides truncatus*). By comparison, 10 normal house sparrows (five males, five females) collected in the same county 1 year later (Ramsey County, Minnesota; May 1982) were host to a mean of 20 lice (range, 0–56) and 38 mites (range, 0–128). In a year-round study of 300 house sparrows in north-western Indiana, McGroarty and Dobson (1974) reported mean loads of 19 *B. subtilis* (range, 0–146) and 62 *P. truncatus* (range, 1–1204). Thus, the louse and mite loads of the deformed sparrow exceeded those of normal birds by more than an order of magnitude!

Birds with deformed or missing feet sometimes have elevated populations of ectoparasites that are restricted to the head and upper body, i.e. those regions that must be groomed with the feet. For example, two one-legged sandpeeps, *Calidris alba*, at Bodega Bay, California had elevated

numbers of nits on their heads and upper breasts, compared to 78 normal sandlings handled at the same site (Myers, personal communication). A one-legged ruddy turnstone, *Arenaria interpres*, in Jamaica also had an unusually large number of lice and nits on the feathers of its head and neck (Tordoff, personal communication). These and other observations suggest that grooming plays an important role in ectoparasite resistance, but they do not control for the possibility that increased loads are due to the poorer general condition of deformed hosts. Proper nutrition and health are critical for ectoparasite resistance (Nelson *et al.* 1975; Nelson 1984).

Ectoparasite increases also have been documented on birds with experimentally impaired preening (Kartman 1949; Nelson and Murray 1971; Brown 1972; DeVaney 1976). In all cases, however, birds were impaired by 'debeaking', viz. removing the distal end of the upper mandible of the bill, which results in a dramatic increase in louse population. Although such studies convincingly demonstrate that preening controls lice, they do not factor out the impact of debeaking-induced stress on louse loads. Stress is known to reduce general resistance to parasites (Esch *et al.* 1975), including ectoparasites (Nelson 1962; Lodmell *et al.* 1970). The goal of experiment I was to measure louse increases on hosts impaired with a less stressful technique, both under natural conditions and captive conditions that maximize the transmission and reproductive potential of lice.

Methods

I impaired the preening ability of pigeons with metal 'bits': small (<0.8 g), C-shaped pieces of plated steel inserted between the mandibles (Fig. 14.3). The bits were crimped slightly in the nostrils to prevent dislodging, but not so far as to pierce the tissue. Bits create a 1.0–3.0 mm gap between the mandibles, preventing the full occlusion of the bill necessary for efficient preening. Birds typically shake their heads for several minutes immediately after receiving bits, but ignore them thereafter. Bits have no detectable effect on the general condition or reproductive performance of rock doves. During a pilot study of captive, louse-free pigeons, the weights and reproductive success of bitted adult pairs did not differ significantly from those of non-bitted pairs (Clayton 1989). Because rock doves feed their young by regurgitation rather than by the forceps-action of the bill typical of most birds, bits do not interfere with the rearing of offspring.

During March–May 1981 I captured 35 wild rock doves from a population of several hundred individuals residing in an abandoned grain elevator in St. Paul, Minnesota. The birds were banded and

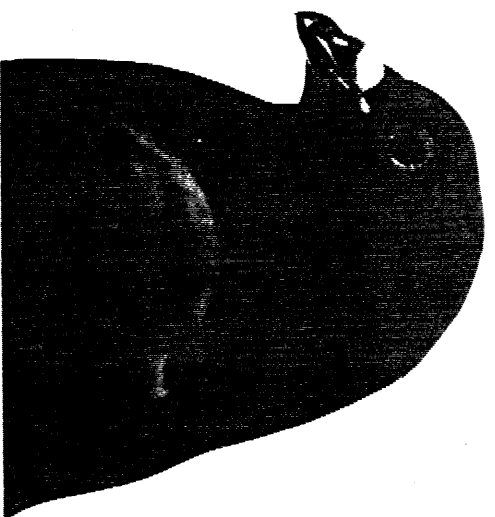


Fig. 14.3. Mandibular displacement of a bitted host.

weighed, then placed in a 2.5 m × 1.5 m × 2.5 m outdoor enclosure constructed of wood and wire mesh, where they were provided with a limited daily supply of cracked corn and *ad libitum* grit and vitamin-supplemented water. The enclosure exposed birds to ambient temperature and photoperiod, but protected them from wind and precipitation. In May, 28 birds were randomly fitted with bits, and seven were designated non-bitted controls. One of the 28 bitted individuals served as a fortuitous control because it was fitted with a bit too thin to create a mandibular gap. In August, after approximately 15 weeks, nine of the captive birds were weighed, killed, and frozen for later censusing of their total louse loads. The nine birds consisted of six bitted and two non-bitted birds selected at random, and the 'control-bitted' bird selected intentionally.

During May–June 1981, I captured, banded and weighed another 41 wild rock doves from the same population. To estimate natural loads, five birds were selected at random, killed, and frozen for louse censuses. The 36 remaining birds were released at the capture site after randomly fitting 23 with bits, and leaving 13 as controls. In September, after approximately 15 weeks, eight birds from the wild population were shot and frozen for louse censuses. Of the eight, two were bitted birds and six were previously uncaptured birds. The mandibles of one of the latter were crossed, a common congenital deformity (Pomerooy 1962).

To isolate the louse populations of frozen birds for censusing total load, I used a modified version of the KOH dissolution technique (Cook 1954; Kim 1972). After thawing, the entire plumage of each bird was

plucked carefully into a beaker, then dissolved in 15 per cent (by weight) KOH solution heated over a Bunsen burner for 15 min. After dissolution, the hot solution was filtered through an 80 mesh stainless steel screen. Undissolved solids were then incubated at 37°C for 24 h in a solution of 3 per cent trypsin (4 × U.S.P. pancreatin), buffered to pH 7.8–8.3 with 0.2 M Na₂ PO₄. This procedure dissolved the host's feathers and attached tissue, but not the chitinous exoskeletons of lice, which were dissecting with the screen, stained in acid fuchsin, and counted under a (range, 91–100 per cent), based on four blind tests with predetermined numbers of adult and nymphal lice (range, 50–520) added to clean feathers. Mean recovery was only 82 per cent (76–93 per cent) in four additional tests using only nymphs (37–89) on clean feathers. Thus, reliability of the technique was less for nymphs than adults, presumably because some nymphs penetrated the screen. I found no indication that nymphal exoskeletons are dissolved by the technique, however, as suggested by Ash (1960).

For statistical analyses louse census data were log transformed to meet the assumptions (homoscedasticity) of multivariate (MANOVA) and univariate (ANOVA) analyses of variance, which were performed using the general linear model procedure (GLM) of the Statistical Analysis Software package (SAS Institute 1985). June and September natural loads were compared non-parametrically (Siegel 1956) because of significantly different variances, despite transformation. Host weight data were analysed non-parametrically for the same reason.

Results and discussion

The *Campanulotes bidentatus* loads of wild, non-impaired rock doves did not change substantially over the summer (Fig. 14.4). The *C. bidentatus* loads of June birds were not significantly different from those of September birds (Mann-Whitney $U = 9$, $p = 0.55$, two-tailed; Table 14.1). *Columbicola columbae* loads, however, showed a highly significant increase on the same birds over the course of the summer ($U = 0$, $p = 0.0009$). This seasonal increase was similar to those reported for other species of avian lice (reviewed in Marshall 1981).

Loads of both *C. bidentatus* and *C. columbae* increased dramatically on the impaired, wild rock doves (one deformed, two bitted) (Fig. 14.4), compared to the non-impaired, wild birds. Both species of lice also increased on the impaired, captive birds (six bitted), compared to the non-impaired captives (two non-bitted, one control-bitted). The effect of host preening ability on each species of louse, for both wild and captive

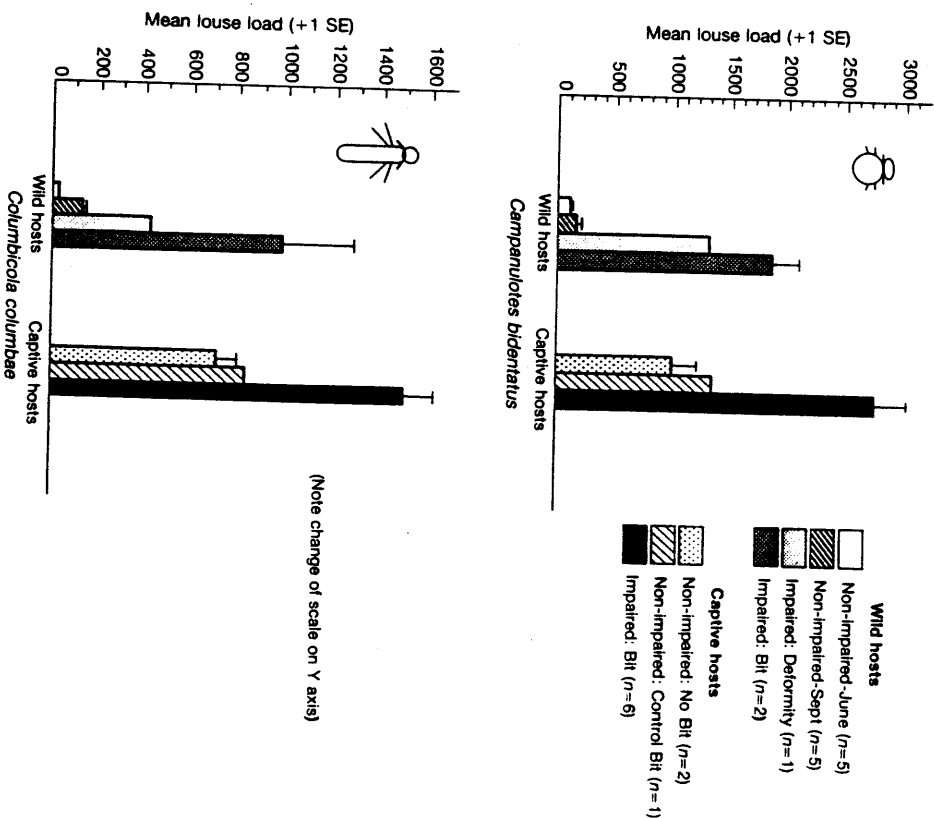


Fig. 14.4. Louse loads of experiment I rock doves.

hosts, was highly significant (ANOVA, $p = 0.0001$; Tables 14.2 and 14.3).

Likewise, a highly significant overall effect of preening on louse load occurred (MANOVA, Wilks' Criterion $F = 49.7$, $p = 0.0001$, $df = 2, 12$). The preening-related increase in the *C. columbae* loads of wild birds was nearly an order of magnitude greater than the seasonal increase in *C. columbae*.

Wild pigeons had fewer lice than captive pigeons (Fig. 14.4): impaired wild birds were host to smaller loads than impaired captives, and non-impaired wild birds were host to much smaller loads than non-impaired

Table 14.1. Mean louse loads and weights of experiment I rock doves (ranges)

Host location & preening ability (N)	<i>Campanulotes bidentatus</i>	<i>Columbicola columbae</i>	Host weight (to nearest 5 g) (g)	May/June	Aug/Sept
Wild: non-impaired					
June (5)	94 (34-130)	21 (5-39)	336 (280-450)	—	—
September (5)	148 (44-287)	133 (91-168)	—	—	430 (390-490)
Wild: impaired					
Deformed (1)	1307	475	—	—	360
Bitted (2)	1847 (1595-2100)	975 (671-1280)	355 (320-390)	400 (350-450)	—
Captive: non-impaired					
Non-bitted (2)	995 (792-1198)	711 (624-799)	405 (400-410)	360 (300-420)	—
Control-bitted (1)	1336	832	410	370	—
Captive: impaired					
Bitted (6)	2749 (1619-3666)	1488 (963-1810)	383 (360-400)	345 (330-370)	—

captives. The effect of host location on both species of lice was highly significant (ANOVA, $p = 0.0001$; Tables 14.2 and 14.3), and a highly significant overall effect of location on louse load occurred (MANOVA, $F = 41.8$, $p = 0.0001$, $df = 2, 12$).

Table 14.2. Analysis of variance, testing the relationship of *Campanulotes bidentatus* load to preening ability (impaired versus non-impaired) and host location (wild versus captive)*

Source of variation	Degrees of freedom	Sums of squares†	Mean square	F
Preening ability	1	2.24068	2.24068	54.90‡
Host location	1	1.30846	1.30846	32.06‡
Preening by location interaction	1	0.52765	0.52765	12.93¶
Model	3	5.33031	1.77677	43.54‡
Error	13	0.53054	0.04081	—
Total	16	5.86085	—	—

* Log transformed data.
 † Type IV sum of squares, reflecting adjustment for other factors in the model.
 ‡ $p < 0.0001$.
 § $p < 0.001$.
 ¶ $p < 0.01$.

Table 14.3. Analysis of variance, testing the relationship of *Columbicola columbae* load to preening ability (impaired versus non-impaired) and host location (wild versus captive)*

Source of variation	Degrees of freedom	Sums of squares†	Mean square	F
Preening ability	1	1.02985	1.02985	59.02‡
Host location	1	1.10651	1.10651	63.41‡
Preening by location interaction	1	0.19650	0.19650	11.26¶
Model	3	3.13229	1.04410	59.84‡
Error	13	0.22684	0.01745	—
Total	16	3.35913	—	—

* Log transformed data.
 † Type IV sum of squares, reflecting adjustment for other factors in the model.
 ‡ $p < 0.0001$.
 § $p < 0.001$.
 ¶ $p < 0.01$.

The larger loads of captive birds probably resulted from several factors. First, the small size and design of the enclosure forced the captive birds to roost side by side in direct contact, probably facilitating louse increases by increasing transmission rates. As a rule, louse populations are larger on birds kept in close quarters (Blagoveshchenskii 1959). Captivity also reduced the efficacy of preening, as indicated by the significant interaction of location and preening ability in the ANOVA for each species of louse ($p < 0.01$; Tables 14.2 and 14.3), as well as the significant overall interaction between location and preening demonstrated by the MANOVA ($F = 10.5$, $p = 0.0023$). This reduction in preening efficiency may have resulted from the poorer general condition of captive birds, whose weights decreased significantly over the course of the experiment (Wilcoxon $T = 1$, $p < 0.01$, two-tailed, $N = 6$ impaired, 3 non-impaired; Table 14.1). This decrease, attributable to the intentionally restricted diet (see methods), did not differ significantly between the impaired and non-impaired captives ($U = 8.5$, $p > 0.44$, one-tailed). Thus, reduced condition was not responsible for the differential increases of lice on impaired versus non-impaired captives.

Reduced general condition was not responsible for the differential increases of lice on the wild rock doves. Weights of the two bitted birds increased over the summer (Table 14.1), and September weights of the three impaired birds did not differ significantly from those of the five non-impaired birds ($U = 3$, $p = 0.18$, two-tailed). The frequency of recapture for the bitted birds (2 of 23) and non-bitted birds (0 of 13) did not differ significantly ($\chi^2 = 1.2$, $p = 0.27$; in this case the null hypothesis was not rejected despite the increased probability of a Type I error due to

expected frequencies < 5; Zar 1984). Subsequent field experiments with bitted birds in Illinois verify that bits do not cause a reduction in general condition during the summer (Clayton 1989).

The louse loads of bitted wild birds did not exceed the maximum loads of wild rock doves in a field study of effects of lice on host reproduction and survival (Clayton 1989). Of 190 wild pigeons (without bits) censused in rural Illinois, six individuals (3.2 per cent) supported loads similar to those on the bitted wild birds in this experiment. The upper mandibles of four of these six wild birds were overgrown by 5–10 mm, and a fifth bird was missing the tip of its lower mandible. The remaining bird showed no obvious deformity. Thus, bite-induced increases mimic naturally occurring increases resulting from bill deformities, which are not uncommon (Rothschild and Clay 1952; Ash 1960; Pomeroy 1962; Ledger 1969).

This experiment demonstrates the important role of preening for louse control, both under natural conditions, and artificial conditions that maximize louse fitness. The effectiveness of preening depends on the conditions of a host's environment, so it is not the only factor influencing louse populations. Preening is clearly an important means of control, however, and may represent the first line of defence against lice and other ectoparasites.

Experiment II: effect and distribution of lice on the host

Defence against parasites is adaptive only if parasites have a negative effect on host fitness. The adaptive function of parasite defence cannot be assumed because many parasites act as commensals much of the time (Noble and Noble 1982). The chief goal of this experiment was to measure the effect of lice on the host, viz. the relationship of louse load to plumage quality. Two additional objectives of the experiment were (1) to determine the relative distributions of *C. bidentatus* and *C. columbae* on the host, and (2) to establish a statistical model for predicting the louse loads of live rock doves from visual counts of specific body regions. These objectives were prerequisites for experiment III (see below).

Methods

Recaptured rock doves under bridges spanning streams in northern Illinois, May–November 1986. The birds were caged individually or in small groups in the loft of a barn at the University of Illinois, Urbana–Champaign. They were provided with commercial grain (Kaytee Breeder and Conditioner Pigeon Feed #6™), grit, and water, and were exposed to

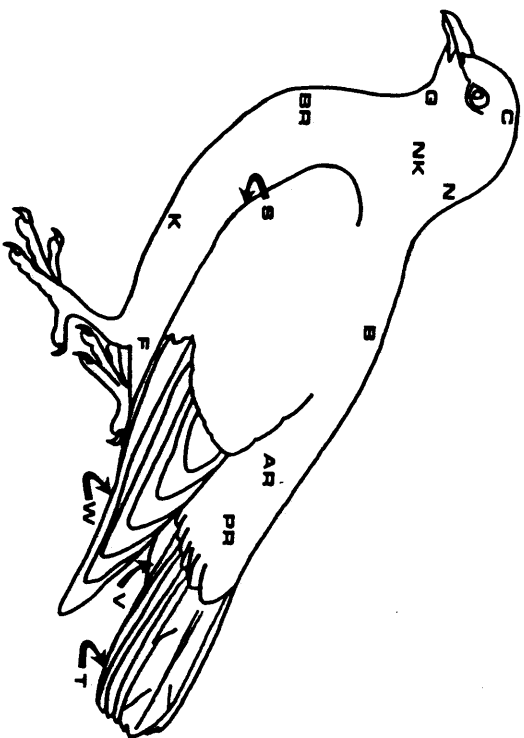


Fig. 14.5. Regions counted for lice and/or sampled for feathers. B, back; BR, breast; C, crown; F, flank*; G, gulum; K, keel; N, nape; NK, side of neck*; AR, anterior rump; PR, posterior rump; S, side* (under wing); T, tail (ventral surface of rectrices); V, ventral caudal tract; W, wing* (ventral surface of remiges). * Indicates counts restricted to one side of the host.

ambient temperature and photoperiod. At least several weeks prior to sampling (see below), all birds were isolated in small cages to prevent them from contacting other birds and to prevent them from flying.

I selected 26 individuals of varying plumage colour and pattern (13 males, 13 females) and bitted 18 of these at various intervals between July and December to create a range of louse loads. The birds were bitted for the following approximate durations: three individuals for 12 weeks, three for 14 weeks, two for 18 weeks, eight for 24 weeks, and two for 34 weeks. Eight individuals were not bitted. In December, 15 of the birds were counted for lice, sampled for feathers, and immediately killed and frozen for censuses of total load (see below). These procedures were repeated in February 1987 for the remaining 11 birds.

I estimated the louse loads of live birds by counting lice on each of the 14 regions illustrated in Fig. 14.5. Counting was performed within 1 m of a bright light, as follows. Each bird was partially immobilized with a Velcro™ strip wrapped once around its tarsi (lower legs). Its right wing was then extended, and lice on the ventral surface of the remiges were counted. The basal region of each remex was observed by first deflecting the underwing covert with forceps. Next, the tail was fanned open, and lice on the ventral surface of each rectrix were counted after deflecting the

