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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). Persistant 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 (Matthysse *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, crenidia, 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 Futuyma (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 1); 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
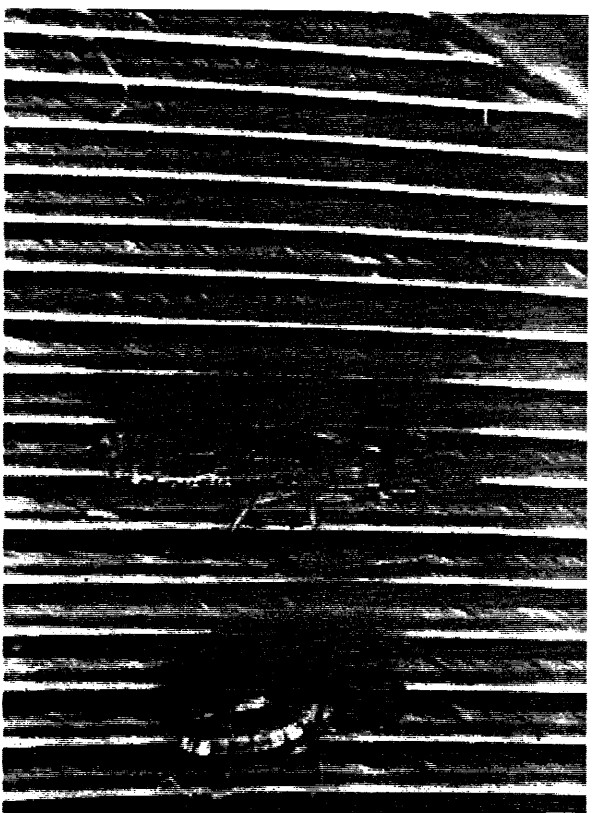

Fig. 14.1. Columbicola columbae (left, 2.5 mm long) and Campanulotes bidentatus (1.5 mm) on the vane of a flight feather. C. columbae uses its large posterior legs (arrows) to orient and run across the ventral surfaces of flight feathers. C. bidentatus, which cannot manoeuvre on flight feathers because 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 *Campanulotes 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, Hellenthal, 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 *Campanulotes* 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 *Physconelloides 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 (*Brüelia subtilis*) and over 400 mites (mostly *Proctophyllodes 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 sanderlings, *Calidris alba*, at Bodega Bay, California had elevated

numbers of nits on their heads and upper breasts, compared to 78 normal sanderlings 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
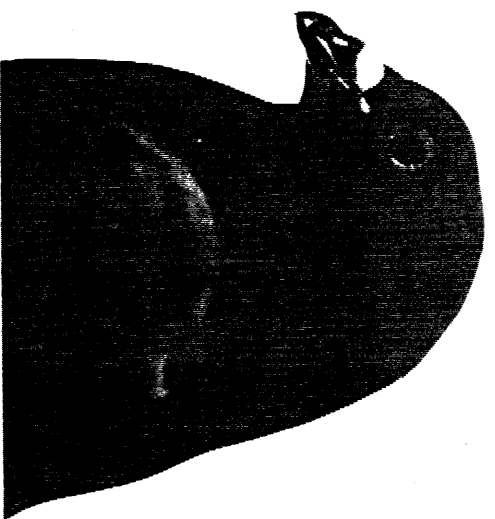

Fig. 14.3. Mandibular displacement of a bitted host.

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 (Pomeroy 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 Na$_2$ PO$_4$. This procedure dissolved the host's feathers and attached tissue, but not the chitinous exoskeletons of lice, which were filtered with the screen, stained in acid fuchsin, and counted under a dissecting microscope. Mean recovery of the technique was 95 per cent (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 ($U = 0$, $p = 0.009$). 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
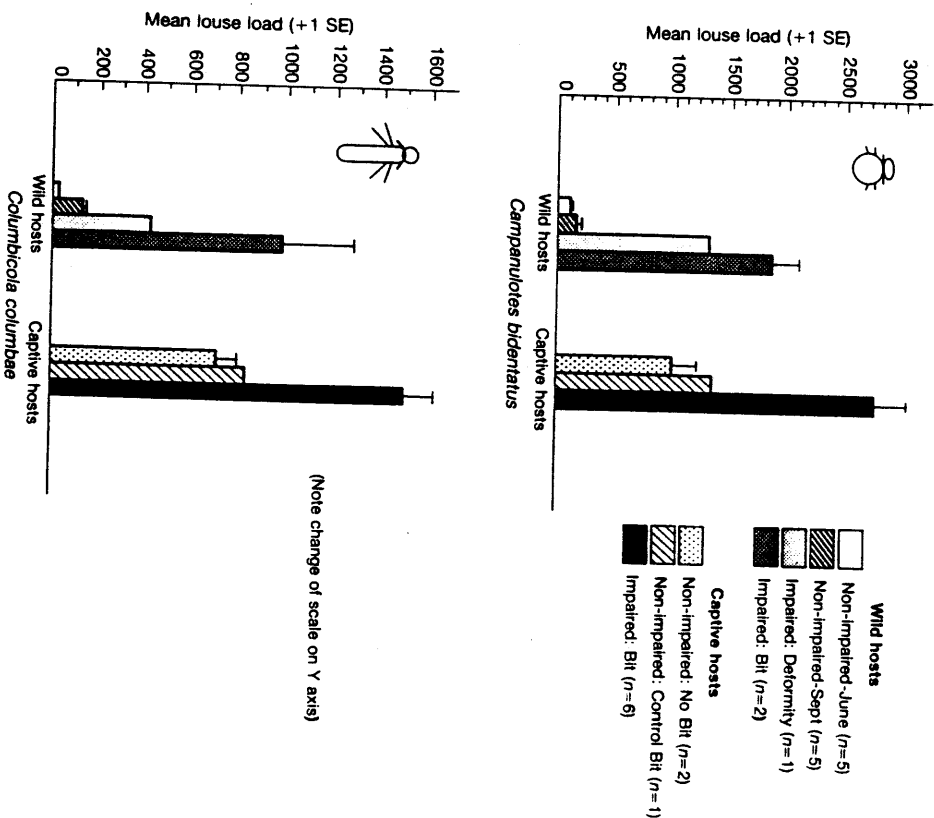

Fig. 14.4. Louse loads of experiment I rock doves.

Mean louse load (+1 SE)

Campanulotes bidentatus — Wild hosts, Captive hosts

Columbicola columbae — Wild hosts, Captive hosts

(Note change of scale on Y axis)

Wild hosts
Non-impaired -June (n=5)
Non-impaired-Sept (n=5)
Impaired: Deformity (n=1)
Impaired: Bit (n=2)

Captive hosts
Non-impaired: No Bit (n=2)
Non-impaired: Control Bit (n=1)
Impaired: Bit (n=6)

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 1 rock doves (ranges)

Host location & preening ability (N)	Campanulotes bidentatus	Columbicola columbae	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)

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

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.
‡ $p < 0.0001$.
¶ $p < 0.01$.

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.
‡ $p < 0.0001$.
¶ $p < 0.01$.

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, $F = 41.8$, $p = 0.0001$, $df = 2,12$).

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, bit-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

I captured 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
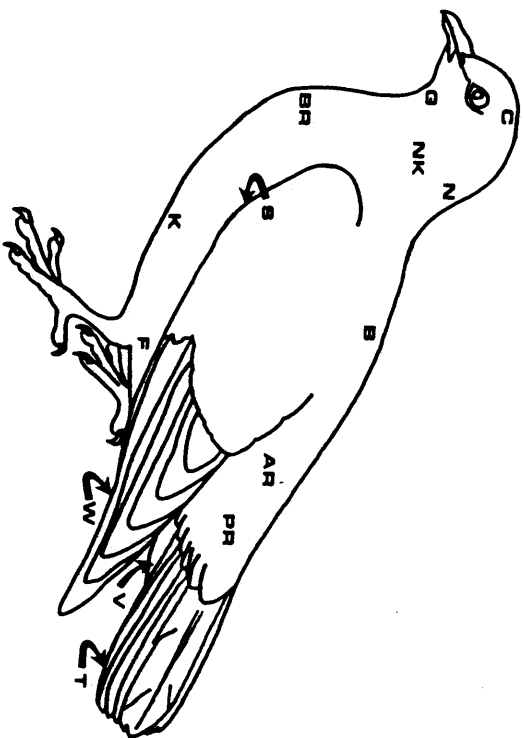

Fig. 14.5. Regions counted for lice and/or sampled for feathers. B, back; BR, breast; C, crown; F, flank*; G. gulum; K, adjacent to keel*; N, nape; NK, side of neck*; AR, anterior rump; PR, posterior rump; S, side* (under wing); T, tail (ventral surface of rectrices); V, ventral caudal tract; W, wing* (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 (see below). In December, 15 of the birds were counted for lice, sampled for feathers, and immediately killed and frozen for censuses of total load. 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

under-tail covert. A timed (30 s) count of each of the remaining regions was made in the following order: vent, keel, breast, gulum, neck, flank, side, crown, nape, back, anterior rump, and posterior rump (Fig. 14.5). The time restriction was necessary because, in contrast to flight feathers (remiges and retrices), it was impossible to examine thoroughly all of the feathers in the regions listed. An attempt was made to observe feathers from throughout each region during its allotted 30-s interval.

I estimated plumage damage by weighing samples of feathers pulled from seven regions: breast, flank, side, nape, back, anterior rump, and posterior rump. Ten feathers were selected haphazardly from each region, and weighed as a group to the nearest 0.001 g. The weights of all seven regions were then added to create a single index of feather weight for each bird.

To isolate the louse populations of frozen birds for censusing total load, I modified the procedure described in experiment I as follows. Birds were skinned in a 1 gallon plastic bucket and the skin with attached plumage was incubated for a mean of 40 h (range, 15–87 hours) in 1–3 per cent buffered trypsin solution. The mixture was then dissolved in 2.5–5 per cent KOH solution heated on a hot plate for up to 4 h. If undissolved feathers or tissue persisted, the procedure was repeated. Exoskeletons were filtered and rinsed with xylene, then 95 per cent ethanol, to eliminate fat adhering to the material (Lemke 1982). The exoskeletons were then stained in acetocarmine and counted. This protocol required one filtration, instead of two, cf. experiment I, and may have reduced the proportion of nymphs passing through the stainless steel screen. The total loads of 23 of the 26 birds were censused successfully using this procedure (the tissue of three birds did not dissolve satisfactorily).

During the regional counts, I observed another species of louse, *Hohorstiella lata* (suborder Amblycera), in large numbers (100s–1000s) on four of the 23 censused birds. Because *H. lata* exoskeletons could not be distinguished reliably from those of *Campanulotes bidentatus*, I omitted these four birds from further consideration, leaving a sample of 19 censused hosts.

Effect of lice on plumage

The relationship between louse load and feather damage was determined by regressing feather weight on total load, after square root transforming the census data to meet the assumptions (homoscedasticity) of least squares regression. Although feather damage accumulates until moult, louse loads fluctuate temporally (Clayton, unpublished data) owing to the depletion of limited food resources and other factors (see experiment III). For this reason, the analysis of load versus damage was restricted to a large group of birds incorporated into the experiment on the same day (nine bitted and four non-bitted individuals; 4 July 1986).

Distribution of lice

Regional distributions of *C. bidentatus* and *C. columbae* were compared using regional count data from the 17 hosts on which at least small numbers of both species of lice were observed.

Prediction of louse load

Regional counts were also used to generate two regression models for predicting the total loads of live birds. First, multiple regression of total census on regional counts was performed for each species of louse (all variables square root transformed; $N = 19$). Regions used as independent variables in the initial *C. bidentatus* regression were vent, keel, breast, neck, flank, side, nape, back, and rump (anterior and posterior rump combined). The wing, tail, gulum, and crown were not used because *C. bidentatus* was never observed on these regions.

All regional counts, except the tail, were included as independent variables in the initial *C. columbae* regression. Although numerous *C. columbae* were observed on the tail early in the experiment (autumn 1986), few were observed during winter counts (December 1986 and February 1987), presumably because *C. columbae* dispersed from the exposed tail (ambient temp $= 0$–$9°C$) to the more protected undersurface of the wings. Because of the extreme seasonal variation in the number of *C. columbae* on the tail the count for this region was subtracted from the total census before using the latter as the dependent variable in the regression. Ultimately, to estimate the total load of a live host, the tail count was added to the prediction of the *C. columbae* regression model (see below). This procedure hopefully reduced the model's sensitivity to changes in ambient temperature.

The final model for each species of louse was generated by subjecting its initial regression to a backward elimination procedure that omitted non-significant variables ($p > 0.01$; Neter et al. 1983). Because this procedure, like other stepwise approaches, does not test all possible combinations of independent variables, it does not necessarily generate the best model. The procedure is sufficient, however, for generating a comparative model to estimate the loads of birds subjected to different experimental treatments (see experiment III).

Results and discussion

The staggered bitting schedule produced the desired range of loads (Table 14.4). *C. bidentatus* and *C. columbae* loads did not differ significantly among the 19 censused hosts ($T = 90$, $p = 0.86$, two-tailed).

Table 14.4. Louse loads and feather weights of experiment II rock doves

Host trait measured (N)	Campanulotes bidentatus			Columbicola columbae			Combined species		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Total louse load (19)	441	570	5–1966	402	456	5–1565	843	800	21–2399
Feather weight (13)	277	256	7–773	394	413	5–1257	671	642	21–2030
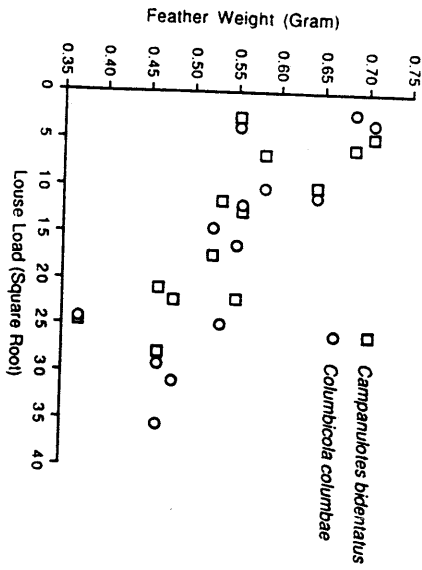
Fig. 14.6. Relationship of feather weight to the number of Campanulotes bidentatus and Columbicola columbae on 13 rock doves.

Effect of lice on plumage

Louse load was inversely related to feather weight (Fig. 14.6). Combined load was a significant predictor of overall feather weight ($r^2 = 0.64$, $p < 0.001$, $df = 12$; adjusted r^2s reported throughout). Combined load also was a significant predictor of regional weight for six of the seven regions sampled ($df = 12$ for all regions): back ($r^2 = 0.53$, $p = 0.003$); breast ($r^2 = 0.50$, $p = 0.004$); flank ($r^2 = 0.56$, $p = 0.002$); nape ($r^2 = 0.27$, $p = 0.04$); side ($r^2 = 0.39$, $p = 0.01$); anterior rump ($r^2 = 0.54$, $p = 0.003$); posterior rump ($r^2 = 0.19$, $p = 0.08$, non-significant). Because C. bidentatus and C. columbae loads were highly correlated ($r = 0.87$, $p < 0.001$, $df = 12$, untransformed data), the separate effect of each species on the plumage could not be determined. Nelson and Murray (1971) showed experimentally that both species depend on the abdominal contour feathers for food. Therefore, both species undoubtedly contributed to the extensive feather damage of birds with high loads.

Clayton (1960b) reported a 23 per cent mean reduction in overall feather weight for a sample of 12 'lousy' rock doves (mean load, 1923;

range, 387–2960), compared to 12 'clean' controls. In the current experiment, mean reduction in feather weight was 28 per cent, comparing weights of the three highest-load birds to weights of the three lowest-load birds. The greater mean damage of the current study probably reflects the fact that the clean birds of the previous study were subjected to some damage prior to the experiment (see Clayton 1990b).

Feather weight, which varies seasonally due to feather wear and replacement, is a useful index of plumage insulation (Calder and King 1974). Barnett (1970) measured a 70 per cent autumn increase in the plumage weights of freshly moulted house sparrows, coinciding with a 12°C increase in their cold tolerance. Conversely, a gradual decrease in feather weight during spring coincided with a reduction in cold tolerance. Reduction in feather weight owing to lice presumably has a similar impact on thermoregulation, and may be responsible for reduced mating success and winter survival of rock doves with large louse loads (Clayton 1989, 1990b).

Distribution of lice

C. bidentatus and C. columbae were observed largely on different regions of the host (Fig. 14.7). These results are in qualitative agreement with
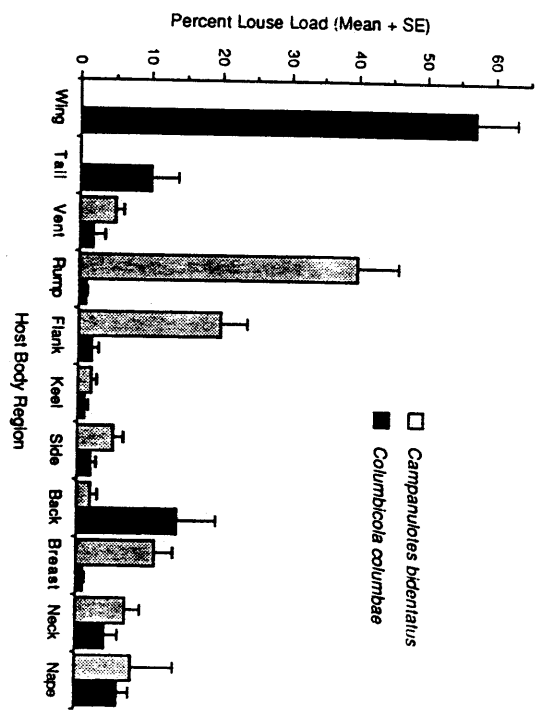

Fig. 14.7. Comparative distribution of lice on 17 rock doves. Data for anterior and posterior rump are combined. Crown and gulum are not displayed because lice were seldom observed in these regions. The data for wing, flank, keel, side, and neck represent one side of the host only. (Percentages calculated within species.)

those of Nelson and Murray (1971), who used a different division of host regions to document the distributions of these species on several rock doves. Approximately 70 per cent of *C. bidentatus* in the current study were observed on the rump, flank, and breast, while approximately 80 per cent of *C. columbae* were observed on the back, tail, and wing. The proportion of *C. columbae* on the remiges and rectrices probably approached 75 per cent, given that 57 per cent were observed on the tail and only one wing. *C. bidentatus*, in contrast, was never observed on the wing or tail. Thus, *C. columbae* is predominantly a wing louse, compared to *C. bidentatus*, which is essentially a body louse. *C. columbae* must spend some time on the body, however, because it depends on abdominal feathers for food. *C. columbae* cannot survive when supplied solely with wing feathers (Nelson and Murray 1971). Although these data are useful for comparative purposes, they do not accurately quantify the microhabitat distributions of the two species, which can only be accomplished with more tedious methods (e.g. Choe and Kim 1988).

Prediction of louse load

Two regression models were generated for predicting the louse loads of live hosts from regional counts. The model for *C. bidentatus* is

$$\hat{y} = 4.11x_1 + 2.14x_2 + 5.54x_3 + 2.77$$

where x_1, x_2, and x_3 are the square roots of the number of lice counted, respectively, on the host's back, rump, and adjacent to the keel ($r^2_{adj} = 0.91$, $p = 0.0001$, $df = 18$). The model for *C. columbae* is

$$\hat{y} = 3.21x + 4.91$$

where x is the square root of the number of lice counted on one wing ($r^2_{adj} = 0.82$, $p = 0.0001$, $df = 18$).

The first model predicts the host's total *C. bidentatus* load. The second model predicts the number of *C. columbae* on the host's back, rump, and adjacent to the keel ($r^2_{adj} = 0.82$, $p = 0.0001$, $df = 18$).

The first model predicts the host's total *C. bidentatus* load. The second model predicts the number of *C. columbae* on the host's total, those on the tail. The number of lice on the tail must be added to the those on the tail. The number of lice on the tail must be added to the square of the number predicted by the model to estimate a host's total *C. columbae* load (see Methods). Because lice on the tail are easy to observe and count, it is unlikely that this procedure reduces the accuracy of the model appreciably.

Experiment III: comparative impact of preening on dissimilar lice

When disturbed by light, streaming air, or simulated preening, *C. columbae* and *C. bidentatus* exhibit different avoidance responses. On a
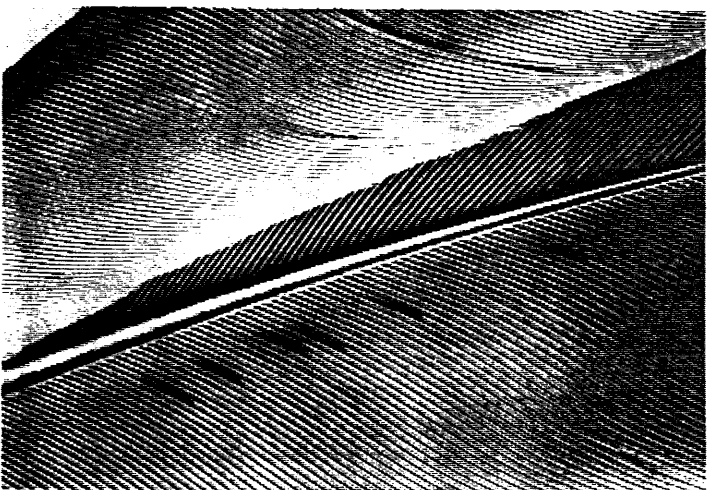

Fig. 14.8. *Columbicola columbae* in typical avoidance posture on a flight feather of the wing. Each louse is inserted between the barbs and oriented toward the shaft, with its mandibles firmly clenched around a barbule. In this position *C. columbae* removes itself from the surface of the feather. (Photo: B. Edinger.)

flight feather *C. columbae* responds to disturbance in at least one of the following ways: (1) it runs rapidly to the base of the feather, where it is hidden by the underwing coverts; (2) it immediately stops moving and flattens itself against the vane; or (3) it inserts itself between two barbs, displacing them with lateral movements of the abdomen, then grasps a barbule firmly between its mandibles. In this position the louse removes itself from the surface of the feather (Fig. 14.8). In an elegant series of experiments, Stenram (1956) demonstrated that *C. columbae* orients to the base of a feather by detecting the directionality of the feather's barbules. Individual lice almost always remain parallel to the barbs of the feather with their heads pointed toward its shaft. If a section of the feather's vane is cut, rotated 180°, and re-attached, individuals placed on the rotated vane orient away from the shaft.

C. bidentatus responds to disturbance on an abdominal contour feather in at least one of two ways: (1) it drops from one feather to

Fig. 14.9. *Campanulotes bidentatus* in avoidance posture on the downy portion of an abdominal contour feather. This species creeps through the downy region at the base of the feather, but remains relatively exposed. (Photo: J. Barabe.)

another; or (2) it creeps to the base of the feather and into the downy region, where it remains relatively exposed (Fig. 14.9). The orientation behaviour of C. bidentatus has not been carefully studied, but it is probably less complicated than that of C. columbae. C. bidentatus seldom leaves the immediate vicinity of a feather's shaft when present on its exposed vane.

Observations such as these suggest that C. columbae is less vulnerable to preening than C. bidentatus. In response to preening C. columbae can run and hide, whereas C. bidentatus can merely run—and more slowly, at that. The avoidance response of C. columbae is not necessarily adaptive for the avoidance of preening, however. Stenram (1956, p. 187) contended that the function of this response is to prevent C. columbae from being blown off the host's feathers during flight, 'When exposed to a stream of air the specimens of C. columbae immediately stop moving and press up to the vane. If the airstream becomes more powerful the specimens force themselves down between the barbs so that only one lateral margin is visible in the vane. On a pigeon the specimens on the distal part of the remiges are mostly found in this position. Here they are exposed to airstreams every time the pigeon flies or flaps its wings. This reaction of the insects has also been released by fastening a remex to a rotating fan.' The goal of the following experiment was to determine whether C. columbae, with its complex avoidance response, is more resistant to preening than C. bidentatus. An additional objective was to compare the selective effect of preening on the morphology of the two species; the results pertaining to this second objective will not be presented here, however.

Methods

During 1986–87, rock doves were captively bred from wild-caught parents in an aviary located in the barn described above (and see Clayton 1990b). Birds several months old were transferred periodically from the aviary to a walk-in enclosure (5.5 × 3.8 × 1.8 m). In May 1987 all birds in the enclosure were bitted, and in late July all birds added to the enclosure since May were bitted, bringing the size of the bitted flock to 175 individuals. Within several weeks of bitting, the louse loads of most birds in the flock were high, owing to the combined effects of the bits and close quarters (4.6 birds/m³, versus 3.7 birds/m³ in experiment I). In late August 18 birds with large louse populations were selected for the experiment, including 8 birds bitted in May and 10 birds bitted in July. The birds were divided randomly into experimental and control groups, each with four May-bitted birds, and five July-bitted birds. They were then placed in 18 cages arranged in pairs, with one experimental bird and one control bird to a pair.

During 2–5 September the louse loads of the 18 birds were estimated from regional counts as described in experiment II. Because one region was inadvertently omitted during the counts (Keel, Fig. 14.5), it was necessary to adopt a modified model for predicting C. bidentatus loads.

$$\hat{y} = 5.83x_1 + 2.25x_2 + 4.27$$

where x_1 and x_2 are the square roots of the number of lice counted, respectively, on the host's back and rump ($r^2_{adj} = 0.81$, $p = 0.0001$, $df = 18$). This model was generated from the multiple regression of total load on the back and rump counts of the experiment II birds. The range of the count data in experiment III exceeded the range of data used in experiment II to generate the predictive models; therefore, the load estimates for birds in experiment III are valid only for comparisons among those birds.

During 6–10 September, approximately 100 C. bidentatus and 100 C. columbae were sampled (removed with forceps) from each of the

□ △ Experimental Birds
■ ▲ Control Birds

Louse Load

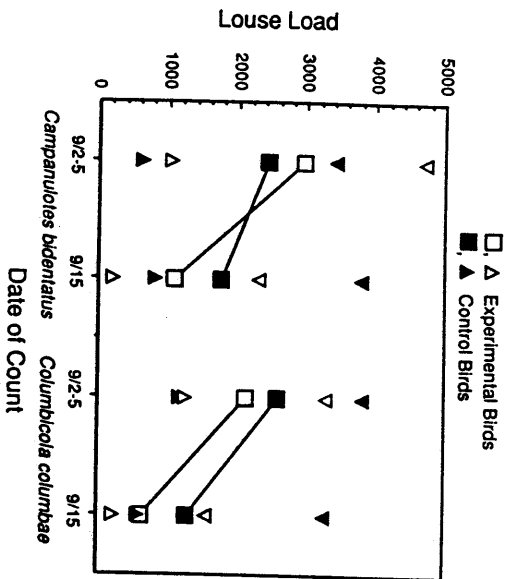Campanulotes bidentatus   Columbicola columbae

Date of Count

Fig. 14.10. Comparative impact of restored host preening on *Campanulotes bidentatus* and *Columbicola columbae*. Squares denote median loads, triangles denote ranges in load, and line segments denote changes in median loads over the course of the experiment. The bits of experimental birds (*n* = 9) were removed 6–7 September; the bits of control birds (*n* = 9) were not removed. The effect of restored preening was significantly greater on *C. bidentatus* than *C. columbae*, suggesting that the complex avoidance response of the latter facilitates escape from host preening.

experimental and control birds for a future study of the selective effect of preening on louse morphology. After sampling, the preening ability of each experimental bird was restored by removing its bit. The preening ability of control birds was not restored; their bits were left in place. On 15 September, the louse loads of all experimental and control birds were again estimated from new counts. The impact of restored preening on each species of louse was determined by comparing changes in the loads of experimental birds to changes in the loads of their paired controls. The relative impact of preening on the two species of lice was determined by comparing their vulnerability to preening on the experimental birds (see below). All comparisons were non-parametric because of significant changes in the variances of loads over time.

Results and discussion

The average louse loads of both groups of birds decreased over the course of the experiment (Fig. 14.10, Table 14.5). This overall decrease, regardless of host treatment, was caused by the sampling of lice and unwanted side-effects of sampling. The sampling procedure required

Table 14.5. Louse loads of experiment III rock doves. Bits were removed from birds in the experimental group, 6–7 September, 1987

Louse species and date, 1987	Experimentals: bits removed (N = 9)				Controls: bits not removed (N = 9)			
	Mean	SD	Median	Range	Mean	SD	Median	Range
Campanulotes bidentatus								
2–5 September	2646	1165	2957	994–4756	2224	944	2431	596–3439
15 September	1046	594	1094	183–2348	1855	957	1779	789–3823
Columbicola columbae								
2–5 September	2199	661	2124	1237–3329	2422	864	2595	1192–3843
15 September	753	517	640	220–1610	1443	804	1288	586–3306

extensive handling of hosts and prolonged exposure to bright light. Handling may have facilitated the transmission of hyperparasites such as *Trenomyces circinans*, a detrimental fungal ectoparasite of *C. columbae* (Eichler *et al.* 1972). Exposure to bright light probably killed large numbers of lice by desiccation (Clayton, unpublished data).

Despite the overall decrease in louse loads due to sampling, there was a significant effect of restored preening on both species of lice. The percentage reduction in the loads of experimental birds exceeded that of controls for both *C. columbae* (Wilcoxon T = 42, p = 0.01, one-tailed) and *C. bidentatus* (T = 45, p = 0.004). Furthermore, preening had a significantly greater impact on *C. bidentatus* than *C. columbae*. The marginal impact of restored preening (percentage reduction on experimental bird minus percentage reduction on paired control) was significantly greater for *C. bidentatus* than *C. columbae* (T = 32, p = 0.025, one-tailed). *C. columbae* showed greater resistance to host preening than *C. bidentatus*, as predicted.

The greater resistance of *C. columbae* to preening is striking, given that this species spends most of its time on the wings (Fig. 14.7), which rock doves preen more than all other regions combined (Fig. 14.11). This result strongly suggests that one adaptive function of *C. columbae*'s avoidance response is escape from host preening. This is not to say that escape is the only adaptive function of the avoidance response; it may also improve the tenacity of lice during host flight and serve other functions.

Conclusions
Adaptive function

The goal of these experiments was to explore the adaptive functions of avian grooming and ectoparasite avoidance. The first experiment verifies
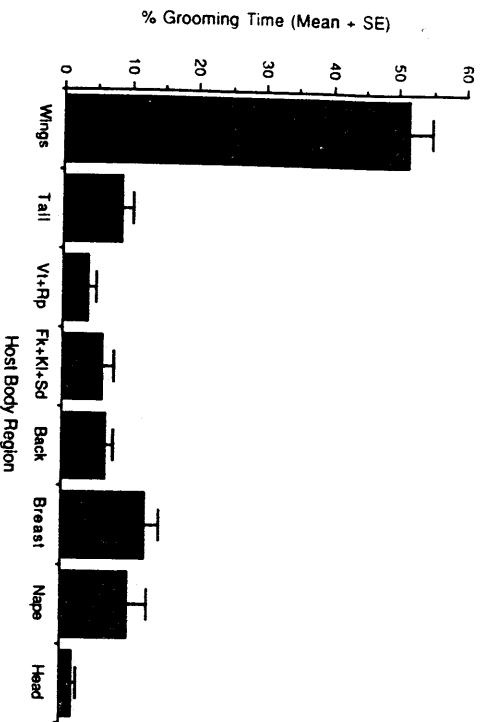
the role of preening in louse control. The second experiment suggests that louse control is adaptive by demonstrating that lice cause extensive plumage damage. The third experiment provides comparative evidence that the avoidance response of C. columbae is adaptive because it facilitates escape from host preening. Taken together, these results suggest that host preening and louse avoidance are reciprocally adapted traits subject to host–parasite coevolution.

Although experiment I demonstrates the effectiveness of preening for louse control, it does not address the mechanics of control. Presumably preening controls lice by removing adults and nymphs from the plumage, but it may also control lice through the direct removal of nits attached to the feathers. Nits are often attached to regions that the host cannot groom, such as the gulum (Nelson and Murray 1971; Marshall 1981). C. columbae nits, which are plainly visible in large numbers on the underwing coverts of rock doves, were not visibly affected by preening in experiment III. However, the direct impact of grooming on the distribution and abundance of nits, as well as the distribution of adults and nymphs, requires detailed study. Also needed is a comparative analysis of the regional efficiency of grooming. The fact that rock doves preen their wings more than other regions may reflect the fact that the remiges are harder to reach than other feathers (Simmons 1964, 1985). The greater impact of preening on C. bidentatus, relative to C. columbae, could

Fig. 14.11. Distribution of grooming by body region. Data are 24 rock doves—12 with large louse loads, and 12 with no lice. Time spent grooming did not differ significantly between the two groups for any region. All regions were groomed by preening, except the head which was groomed by scratching. See Clayton (1990b) for details.

conceivably reflect variation in the efficiency of host defence, rather than variation in the ability of lice to escape host defence.

Experiment II documented the relationship between louse load and feather weight, the latter being a useful index of plumage insulation. Louse-imposed feather damage may reduce the thermoregulatory ability of the host, which would presumably have a negative impact on host fitness (see below). The metabolic cost of lice could be measured by comparing the thermoregulatory ability of birds with different louse loads. If possible, the metabolic cost of grooming behaviour also should be measured to determine more completely the impact of lice on host energetics.

Experiment III provided comparative data suggesting that the avoidance response of C. columbae is adaptive for escape from host preening. Although comparative data can serve as circumstantial evidence, they cannot demonstrate adaptive function. The function of the avoidance response could be demonstrated by measuring its direct contribution to escape ability, preferably in conjunction with experimental manipulation of the avoidance response.

Reciprocal selection and coevolutionary response

Functional and comparative analyses can identify the members of an adaptive complex, but they cannot provide direct evidence of selection or adaptation (Arnold 1983). The adaptive function of a trait may be due to chance, or indirect selection (Williams 1966; Gould and Vrba 1982; Endler 1986). For example, the louse-control function of preening may be an incidental effect of preening for general feather maintenance (Simmons 1964, 1985). Adaptation can be inferred most convincingly by documenting selection on adaptive, heritable traits. Likewise, coadaptation can be inferred by documenting reciprocal selection on the adaptive, heritable traits of interacting species (Schemske 1983, Gould 1988). Manly (1985), Endler (1986), and Price and Boag (1987) review recently derived techniques for the measurement of selection.

Clayton (1989) demonstrated a selective effect of lice on wild rock doves subjected to experimentally increased louse loads. The experimental increases mimicked natural increases on rock doves with inhibited preening resulting from minor bill deformities. Although experimental increases had no effect on the reproductive success of established pairs of rock doves in the field or aviary, they reduced the winter survival of wild individuals, presumably owing to the thermoregulatory cost of feather damage. Feather damage was also apparently responsible for reduced courtship display by lousy males during captive mate choice trials, trials in which lousy males obtained significantly fewer mates than louse-free

males (Clayton, 1990*b*). These results show that experimentally increased louse loads impose direct selection on rock doves via reduced survival, and indirect selection via their influence on host sexual selection.

Lice probably exert selection against natural bill deformities, given that the louse loads of deformed birds are much higher than those of birds with normal bills. Lice may also exert selection on the preening ability of birds with normal bills. This hypothesis could be tested by measuring the covariation of preening and louse load among hosts with normal bills. Before attempting this, however, it will be necessary to develop repeatable methods for measuring minute variations in preening ability. If preening ability covaries with bill morphology, as shown for avian foraging ability (Boag and Grant 1981), it may be feasible to test the selection hypothesis by measuring the covariation of bill morphology and louse load.

Although the selective effect of lice on rock doves has been demonstrated, the hypothesized reciprocal effect of host grooming on lice has not been tested. Grooming may eliminate lice purely at random, in which case it can have no direct effect on the evolution of louse avoidance. By contrast, if grooming eliminates lice selectively, it can directly influence the evolution of avoidance, assuming avoidance is a heritable trait (see below). The intensity of grooming-imposed selection is likely to vary among species of lice with different avoidance mechanisms. For example, it is possible that preening exerts selection on wing lice, but not on body lice which may rely on the density of the abdominal plumage to escape preening purely by chance. Comparing the intensity of preening-imposed selection on *C. columbae* versus *C. bidentatus* would provide a compelling test of this hypothesis.

A final issue that must be addressed in studies of coevolution is genetic response. Selection acts at the phenotypic level and may or may not cause evolution, which is change at the genotypic level (Haldane 1954; Lande and Arnold 1983). Selection can lead to an evolutionary response only if it influences heritable traits. For example, if grooming behaviour has no heritable component it will not coevolve with louse avoidance, regardless of the intensity of louse-imposed selection on the host. The stereotyped variation in grooming among closely related species of birds (e.g. McKinney 1965; Schreiber 1977) suggests that grooming has a genetic component. However, interspecific comparisons of this kind convey little information regarding the narrow-sense heritability required for evolution (Hailman 1986). Heritable variation can be measured using quantitative genetic techniques (Boag and van Noordwijk 1987; Falconer 1989).

In conclusion, the opportunity for coevolution can be thoroughly assessed by documenting reciprocal selection between interacting species, and the potential for coevolutionary response to selection. First, however, one must identify realistic targets of selection by demonstrating the adaptive functions of apparent coadaptations. The evidence presented in this chapter suggests specific adaptive functions for avian grooming and ectoparasite avoidance, and confirms these traits as excellent candidates for coevolutionary analysis. Further assessment of the opportunity for coevolution of grooming and avoidance requires: (1) direct measurement of grooming-imposed selection on ectoparasites; and (2) quantitative genetic analysis of host grooming and ectoparasite avoidance. Rock doves and their chewing lice constitute a realistic system for performing these steps in the near future.

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