Brett R. Moyer · David W. Gardiner · Dale H. Clayton

Impact of feather molt on ectoparasites: looks can be deceiving

Abstract Animals possess a variety of well-documented defenses against ectoparasites, including morphological, behavioral, and immune responses. Another possible defense that has received relatively little attention is the shedding of the host's exterior. The conventional wisdom is that ectoparasite abundance is reduced when birds molt their feathers, mammals molt their hair, and reptiles shed their skin. We carried out an experimental test of this hypothesis for birds by manipulating molt in feral pigeons (*Columba livia*) infested with feather lice (Phthiraptera: Ischnocera). We used two standard methods, visual examination and body washing, to quantify the abundance of lice on the birds. The visual data indicated a significant effect of molt on lice. However, the more robust body washing method showed that molt had no effect on louse abundance. Two factors caused visual examination to underestimate the number of lice on molting birds. First, molt replaces worn feathers with new, lush plumage that obscures lice during visual examination. Second, we discovered that lice actively seek refuge inside the sheath that encases developing feathers, where the lice cannot be seen. The apparent reduction in louse abundance caused by these factors may account for the conventional wisdom that feather molt reduces ectoparasite abundance in birds. In light of our experimental results, we argue that it is necessary to reinterpret the conclusions of previous studies that were based on observational data. Additional experiments are needed to test whether shedding of the host's exterior reduces ectoparasites in other birds, mammals, and reptiles, similar to the impact of facultative leaf drop on herbivorous insects on trees.

Keywords Ectoparasites · Feather molt · Host defense · Lice

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Introduction

"The problem of the effect of animal's molting on their infestation has been little studied so far but it can play, no doubt, an important role in reduction of infestation since both parasites and their eggs are thrown off together with molting feathers and hairs." (Blagoveshchensky 1959).

More than half of all animal species make their living as parasites of other species (Price 1980). The pervasiveness of the parasitic lifestyle has selected for a wide variety of defenses in animal hosts. Examples range from immune responses to anti-parasite behavior, such as grooming (Hart 1990; Wikel 1996). Another possible defense, which has received less attention, is the shedding of the host's exterior. A diverse group of animals regularly molt, including birds, mammals, and reptiles. The conventional wisdom is that molt reduces ectoparasite infestations, in addition to replacing worn feathers, hair, or skin (Marshall 1981; Kim 1985; Lehane 1991). Several studies of lice on mammals and birds have provided observational data showing apparent reductions in louse abundance coincident with molt (Murray 1957; Blagoveshchensky 1959; Baum 1968). For example, Murray (1957) documented an 80% reduction in louse eggs on molting domestic horses, and Baum (1968) reported an 85% drop in the abundance of hatched lice on molting Eurasian blackbirds (*Turdus merula*).

An experimental approach is needed to firmly test the effectiveness of molt as a means of reducing ectoparasite populations. It is conceivable that the reductions documented in earlier studies were caused by unidentified variables that covary with molt. For instance, Markov (1940) observed a decrease in the number of ectoparasites on Starlings (*Sturnus vulgaris*) during the autumn. He argued that feather molt caused this decrease, but Boyd (1951) argued that coincident, seasonal changes in climate were responsible. In this paper we report the results of an experiment designed to test the impact of feather molt on lice. We used shortened photoperiod to induce molt in experimental birds. We then compared the

abundance of feather lice on molting birds to that on non-molting control birds over a period of 3 months.

The experiment utilized feral pigeons (*Columba livia*), also known as rock doves, and two species of host-specific, feather-feeding lice (Phthiraptera: Ischnocera). The lice were *Columbicola columbae*, a "wing" louse that lays its eggs and spends much of its time on the wings, and *Campanulotes bidentatus compar*, a "body" louse that lives on abdominal regions such as the rump and back (Nelson and Murray 1971; Clayton 1991a; Clayton et al. 1999). Both species are "permanent" ecto-parasites that carry out their entire life cycle (ca. 1 month) on the host. Louse eggs are glued to the feathers with a glandular cement and typically hatch in less than a week (Marshall 1981). For transmission to new hosts the two species require direct contact between host individuals (Clayton and Tompkins 1994). The close association of lice with the host presumably increases their vulnerability to being lost on molting feathers.

All birds periodically replace worn plumage by molting, during which new feathers develop and push the old ones out of their follicles (Payne 1972; Welty and Baptista 1988). Most species of birds molt once a year, often immediately after the breeding season. Although the most important function of molt is to maintain the plumage in good condition for efficient insulation and flight (Payne 1972; Welty and Baptista 1988), a secondary function may be to jettison ectoparasites.

Reducing the abundance of lice and other ectoparasites is important to birds (Møller et al. 1990; Lehmann 1993). The lice we studied feed on feathers and dermal debris. The feather damage they cause interferes with the bird's thermoregulation, leading to a compensatory increase in metabolic rate (Booth et al. 1993), a steady decrease in body mass, and a significant reduction in overwinter survival (Clayton et al. 1999). Accordingly, lice are a selective agent for the evolution of efficient host defense. The goal of our study was to test whether molt is one such defense. If so, then additional hypotheses await testing. For example, female birds of several species are known to prefer louse-free males (reviewed in Clayton 1991b), and some of these species undergo a molt immediately before the breeding season (Stresemann and Stresemann 1966; Welty and Baptista 1988). Assuming molt reduces lice, the timing of this prenuptial molt could be a result of selection to reduce louse abundance prior to the mating season.

Materials and methods

Twenty feral pigeons were captured using walk-in traps baited with grain at several sites in Salt Lake City, Utah. The birds were maintained on a 12-h photoperiod in our animal facility at room temperature and at 50% relative humidity. They were housed individually in wire mesh cages and provided ad libitum with grain (Wheatland Seed, Pigeon Mix), grit, and water.

Birds control ectoparasites by disabling or removing them with the bill during preening (Hart 1997). One consequence of molt is irritation to the skin, which can lead to an increase in maintenance behaviors such as anting and sunning (Potter and Hauser 1974). If

molt also leads to an increase in preening, that increase may reduce louse abundance even if molt itself has no direct effect on lice. To isolate the potential effect of molt on lice, we blocked preening in all of the birds in our study by fitting them with bits shortly after capture. Bits are C-shaped pieces of plastic developed by the poultry industry. They are inserted between the upper and lower mandibles and crimped slightly in the nostrils to prevent dislodging, but without damaging the tissue. Bits create a 1–3 mm gap between the mandibles that impairs the forceps-like action of the bill required for efficient preening. Bits do not interfere with feeding and have no side effects on the bird (Clayton and Tompkins 1995). Bits have been used to manipulate preening in several previous experiments with pigeons and lice (Clayton 1991a; Booth et al. 1993; Clayton and Tompkins 1994, 1995; Clayton et al. 1999).

Previous work indicated that only 46% of pigeons have lice at the study site (*n*=455 birds, unpublished data). To ensure that all of the birds in our experiment were parasitized, we "seeded" them with lice obtained from stocks maintained on culture pigeons in our lab. Each bird was seeded with 20 *Columbicola columbae* and 20 *Campanulotes bidentatus compar*, which supplemented any lice the birds already had when captured.

The seeding process was as follows. Culture birds were placed in a CO_2 chamber with a collar through which the bird's head protruded (Visnak and Dumbacher 1999; Clayton and Drown, 2001). Lice on the body and wings were exposed to a stream of CO_2, while the bird's head was exposed to a stream of fresh air outside the chamber. This procedure anesthetized the lice, which fell onto filter paper at the bottom of the chamber. Additional lice were removed by ruffling the feathers of the bird over a sheet of white paper. Once the lice revived (ca. 5 min), they were removed from the paper with a soft brush and placed on an isolated feather. The feather was then inserted under the feathers of a recipient bird, which was restrained for 1 h to allow the lice to position themselves in appropriate microhabitats on the host. Each bird was restrained by securing its legs with a Velcro strip, then sliding it into a cardboard cylinder (oatmeal box, 10 cm diameter×18 cm long with breathing holes). After seeding, birds were returned to their individual cages and maintained on a 12-h photoperiod for 3 months. The 3-month period allowed the birds to acclimate fully to captivity and provided time for their lice to establish and multiply. Seeding had the desired effect; after 3 months all 20 birds had established louse populations, with means (±1 SE) of 655 (±85) wing lice and 590 (±62) body lice per bird (visual examination method; see below).

To investigate whether feather molt reduces ectoparasites, we took advantage of the fact that the onset of molt is triggered by the decreasing day length associated with autumn (Payne 1972; Dawson 1994, 1998). We manipulated the photoperiod of experimental birds to induce feather molt, and we assessed the impact of this molt on their lice. First, we increased the photoperiod for all 20 birds from 12 to 13 h of daylight. After several weeks at 13 h, we randomly assigned 10 experimental (molt) birds to a reduced photoperiod of 8 h daylight, while continuing to expose 10 (control) birds to 13 h of daylight. The experimental and control birds were housed in adjacent rooms maintained at these different photoperiods by electric timers. Visual examination (see below) showed no significant difference in the mean number of lice on birds assigned to the two treatments (wing lice: t=0.51, df=18, P=0.62; body lice: t=0.10, df=18, P=0.92).

Like most birds, feral pigeons molt the large flight feathers of the wings and tail more gradually than the core body feathers. Flight feathers are molted over a period of about 5 months, whereas body molt requires only 3 months (Johnston and Janiga 1995). Body molt normally begins more than a month after initiation of flight feather molt. We used the primary feathers of one wing as an index of flight feather molt, which is concurrent on the two sides of the body. Primary molt in feral pigeons begins with the innermost primary (p1) and ends when the outermost primary (p10) is dropped. We kept track of the progression of flight feather molt by periodically recording the most recent primary feather to have been dropped (Fig. 1a).

We tracked body molt by periodically estimating the percentage of new "pinfeathers" emerging in each of 11 body regions:
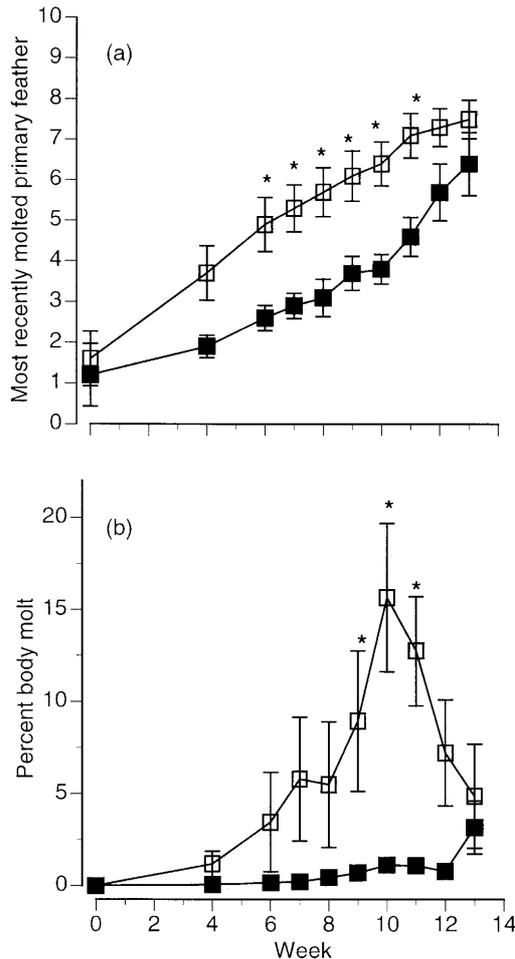
Fig. 1 Change over time in the mean (±1 SE) **a** stage of primary molt and **b** percent body molt, on molt (*open squares*) and control (*closed squares*) birds. The distributions of primary and body molt scores were non-normal and transformations did not normalize the data; therefore we compared the molt scores for the two treatments at each week using Mann-Whitney tests [* denotes a significant difference following sequential Bonferroni adjustment (Rice 1989) of α=0.05 for *k*=10 comparisons]

vent, rump, back, breast, keel, flank, side, nape, neck, crown, gulum (see Fig. 1 in Booth et al. 1993). The values for each of these regions were averaged to produce an overall body molt score for each bird (Fig. 1b).

At the start of our experiment (week 0) about half of the birds in each treatment were already molting their flight feathers. The two groups did not differ significantly in primary molt at this time (Mann-Whitney test, Z=0.97, P=0.33). None of the birds in either treatment had initiated body molt at the start of the experiment.

Manipulation of photoperiod ultimately had the desired effect: molt was greater in experimental birds than controls over the course of the experiment (Fig. 1a, b). The experiment was terminated at week 13, 1 week after the molt scores of experimental and control groups no longer differed significantly (Fig. 1a, b). At this time all birds in the experiment were sacrificed, placed in individual plastic bags, and frozen for quantification of their lice.

Quantification of lice

We used two methods to quantify the abundance of lice on birds. The first method, visual examination, provided an estimate of lice over the course of the experiment on live birds. A second, more

accurate, body washing method was used to compare the abundance of lice on dead birds at the end of the experiment. Both methods use regression models to predict the total abundance of lice from the subsample observed or removed (see below).

Visual examination

We estimated wing lice using a multivariate regression model that predicts total abundance from the number of wing lice observed during a comprehensive (ca. 1 min) examination of the undersurfaces of one wing and the tail (r²=0.73, P<0.0001; Clayton and Drown, 2001). We estimated body lice using a similar model that predicts total abundance from the number of body lice observed during 30-s examinations of the back and keel, and a 60-s examination of the rump (r²=0.87, P<0.0001; see Clayton and Drown, 2001).

Body washing

We also estimated wing and body lice using univariate regression models that predict the total abundance of each species from the number of lice removed by body washing (r²=0.99, P<0.0001 for both species; Clayton and Drown, 2001). This approach, which is somewhat more reliable than visual examination, works like a washing machine. The dead bird was placed in a paint can filled with a mild detergent solution. The can was then shaken vigorously on a mechanical paint shaker for a 10-min "wash" cycle. The bird was transferred to a second can of water and shaken for a 10-min "rinse" cycle. The fluid contents of both cans were filtered to retrieve lice. Body washing is a more accurate estimator of total louse abundance than visual examination, but it can only be used on dead birds (Clayton and Walther 1997; Clayton and Drown, 2001).

Data analysis

The data on louse abundance were normalized prior to analysis using log transformations. Data were analyzed separately for (1) all lice, (2) body lice, and (3) wing lice.

Visual examination data

We assessed the effect of molt on louse abundance using a 2 (treatment: molt, control)×10 (weeks) ANOVA with repeated measures on the second factor (weeks). If there was a significant week×treatment interaction, we also investigated the effect of molt each week using a Protected *t* procedure (Fisher's Least Significant Difference Test) (Howell 1989).

Body washing data

In contrast to the visual examination data, body washing estimates of louse abundance were available only at the end of the experiment for dead birds (week 13). A visual examination was also made immediately prior to sacrificing each bird for body washing. We assessed the effect of molt on louse abundance using a 2 (treatment: molt, control)×2 (quantification method: body washing, visual examination) ANOVA with repeated measures on the second factor. Where appropriate, we also investigated the effect of molt on the louse estimates for each quantification method using the Protected *t* procedure.

Results

Visual examination data

All lice

Figure 2a shows the change over time in the number of lice on birds in each treatment. The 2×10 ANOVA
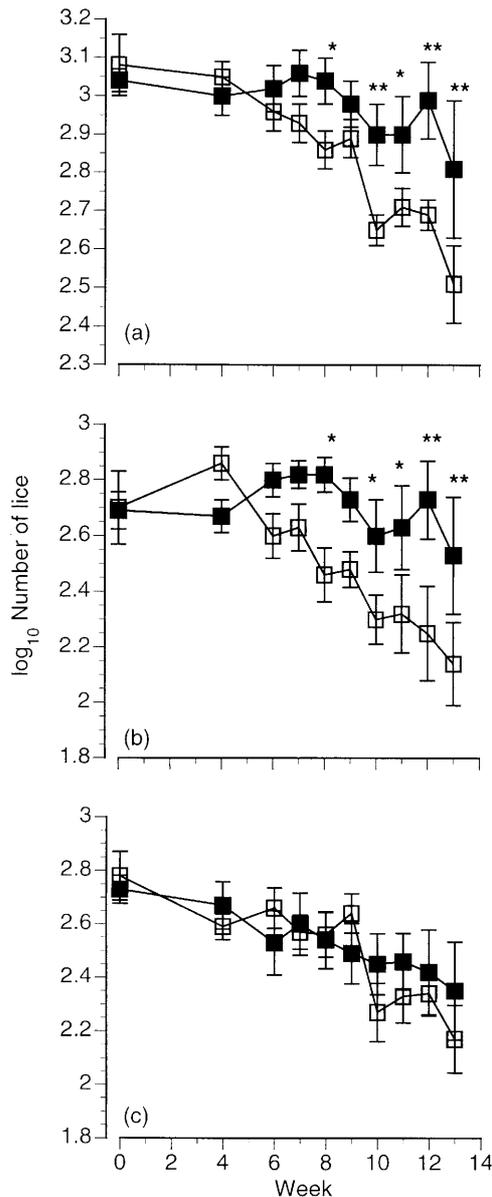
Fig. 2 Change over time in the mean (±1 SE) number of lice estimated by visual examination on molt (*open squares*) and control (*closed squares*) birds: **a** all lice, **b** body lice, **c** wing lice. (Note different *y-axis* in **a**; see text for details) (*$P<0.05$, **$P<0.005$)

Table 1 Repeated-measures ANOVA of the effects of molt treatment and week on the (log) estimated number of: *a* all lice, *b* body lice, and *c* wing lice (visual examination data)

Source	df	SS	F	P
a. All lice				
Treatment	1	0.98	3.50	0.08
Subject	18	5.03	...	...
Week	9	2.92	10.3	<0.0001
Week×Treatment	9	0.73	2.59	0.01
Week×Subject	162	5.11	...	...
b. Body lice				
Treatment	1	2.62	6.24	0.02
Subject	18	7.55	...	...
Week	9	3.63	4.41	<0.0001
Week×Treatment	9	1.76	2.14	0.03
Week×Subject	162	14.8	...	...
c. Wing lice				
Treatment	1	0.05	0.07	0.79
Subject	18	12.5	...	...
Week	9	4.17	10.0	<0.0001
Week×Treatment	9	0.63	1.51	0.15
Week×Subject	162	7.47	...	...

(Table 1 b) revealed a significant main effect of molt, and a highly significant main effect of week, on the number of body lice. As before, there was a significant week×treatment interaction, so the effect of treatment was clarified for each week with the Protected *t* procedure: birds in the molt treatment had significantly fewer body lice than control birds in weeks 8 and 10–13 (Fig. 2b, $t>1.975$, $df=162$, $P<0.05$).

Wing lice
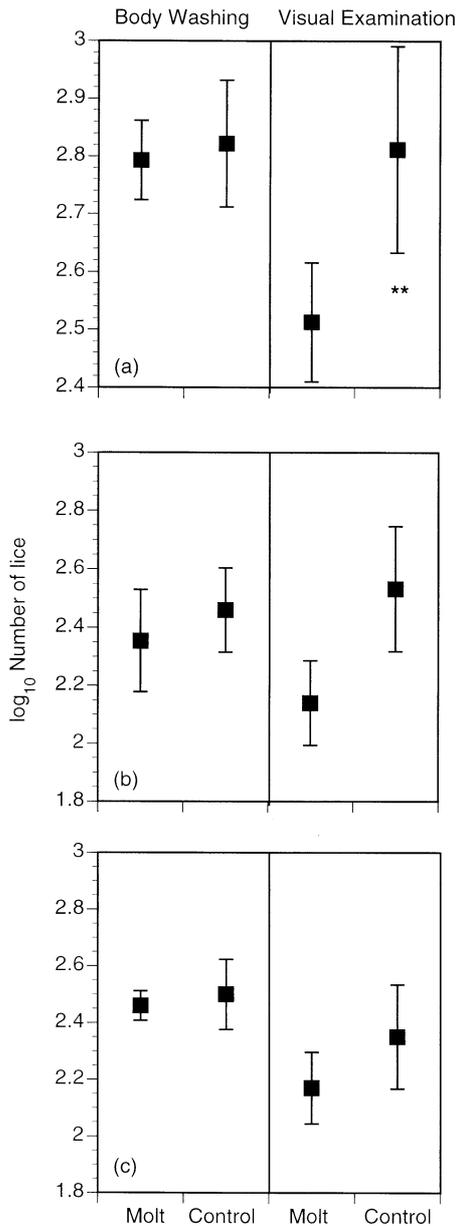
Figure 2c shows the change over time in the number of wing lice on birds in each treatment. The 2×10 ANOVA (Table 1 c) revealed no main effect of molt, but a highly significant main effect of week on the number of wing lice. There was no significant week×treatment interaction.

Body washing data

All lice

Figure 3a shows the number of lice on birds in each treatment at the end of the experiment (week 13), as determined both by body washing and visual examination. The 2×2 ANOVA (Table 2 a) revealed no main effect of molt, but a significant main effect of quantification method on the number of lice. Because there was also a significant method×treatment interaction, the effect of molt was clarified for each quantification method using the Protected *t* procedure. Birds in the molt treatment had significantly fewer lice than control birds when the visual examination data were analyzed (Fig. 3a, $t=3.57$, $df=18$, $P<0.005$), but *not* when the body washing data

(Table 1 a) revealed a nearly significant main effect of molt, and a highly significant main effect of week, on the number of lice. Because there was also a significant week×treatment interaction, the effect of treatment was clarified for each week using a Protected *t* procedure: birds in the molt treatment had significantly fewer lice than control birds in weeks 8 and 10–13 (Fig. 2a, $t>1.975$, $df=162$, $P<0.05$).

Body lice

Figure 2b shows the change over time in the number of body lice on birds in each treatment. The 2×10 ANOVA

Body Washing   Visual Examination

Fig. 3 Mean (±1 SE) number of **a** all lice, **b** body lice, and **c** wing lice, on molt and control birds at the end of the experiment as estimated by body washing and visual examination. Post hoc multiple comparisons were warranted for **a**, but not for **b** or **c** (see text)(**P<0.005)

Table 2 Repeated-measures ANOVA of the effects of molt treatment and quantification method on the (log) estimated number of: *a* all lice, *b* body lice, and *c* wing lice

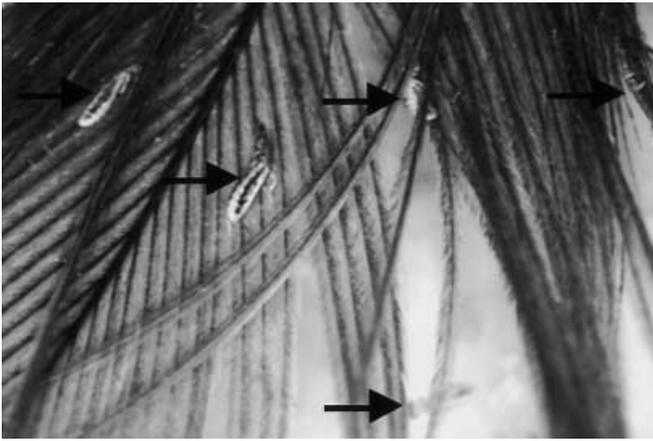| Source	df	SS	F	P
a. All lice				
Treatment	1	0.27	1.03	0.33
Subject	18	4.75	...	...
Method	1	0.21	6.00	0.025
Method×Treatment	1	0.18	5.19	0.035
Method×Subject	18	0.63	...	...
b. Body lice				
Treatment	1	0.62	1.17	0.29
Subject	18	9.51	...	...
Method	1	0.05	0.73	0.40
Method×Treatment	1	0.21	3.03	0.10
Method×Subject	18	1.22	...	...
c. Wing lice				
Treatment	1	0.11	0.39	0.54
Subject	18	5.06	...	...
Method	1	0.49	8.85	0.01
Method×Treatment	1	0.05	0.91	0.35
Method×Subject	18	1.00	...	...

Wing lice

Figure 3c shows the number of wing lice on birds in each treatment at the end of the experiment as determined both by body washing and visual examination. The 2×2 ANOVA (Table 2 c) revealed no main effect of molt treatment, but a significant main effect of quantification method on the number of lice. There was no method×treatment interaction.

Discussion

We manipulated molt on louse-infested pigeons to test the conventional wisdom that molt reduces ectoparasite abundance. Visual examination, which is normally an accurate predictor of louse abundance (see Materials and methods), suggested a significant reduction in the abundance of lice on molting birds. In contrast, body washing showed that molt did *not*, in fact, reduce abundance. The reason for the discrepancy was that molt altered both plumage appearance and louse behavior, which caused us to visually underestimate lice on molting birds.

Plumage appearance played a role because it is more difficult to see lice in new, lush body feathers, compared to worn feathers, particularly those fed upon for many months by feather lice (see Fig. 2 in Clayton 1990). Visual data on body lice showed an apparent drop in abundance (Fig. 2b), whereas those for wing lice showed no such drop (Fig. 2c). The reason for this difference is that wing lice were censused on the surfaces of flight feathers of the wings and tail (see Materials and methods), which are as easily examined when fresh, as when worn. The apparent drop in body lice was responsible for the apparent drop in overall louse abundance (Fig. 2a).

Louse behavior also contributed to the apparent drop in the abundance of body lice on molting birds. We

were analyzed (Fig. 3a, *t*=0.346, *df*=18, *P*>0.50, Power=0.65).

Body lice

Figure 3b shows the number of body lice on birds in each treatment at the end of the experiment, as determined both by body washing and visual examination. The 2×2 ANOVA (Table 2 b) revealed no main effects or interaction involving molt treatment or quantification method.

Fig. 4 Photograph of a dissected, developing pinfeather showing five wing lice using the interior of the furled sheath as a refuge (*scale*: length of *arrows*=1.5 mm). We pulled body feathers from several molting pigeons and incised them longitudinally under a dissecting scope to check for lice. Lice were found in 7 of 30 (23%) of the feathers we dissected (totals: 6 wing, 5 body lice). Although most of the lice were found only a few millimeters inside the mouth of the furled pinfeather, some lice were found deep inside the shaft

discovered, quite by accident, that lice use the interior of developing, unfurled "pinfeathers" as a refuge (Fig. 4), where they are impossible to observe. This behavior provides at least three potential advantages: (1) newly growing feathers are the best places to avoid being discarded on a molting feather; (2) pinfeathers provide a refuge from host preening; and (3) pinfeathers provide a fresh, new source of food. We wonder if the use of pinfeathers as refuges is an early step in the evolution of quill lice, which spend most of their lives inside the quills of mature feathers (Rothschild and Clay 1952). The extreme similarity in the number of lice recovered from molt and control birds by body washing (Fig. 3a) indicates that washing extracts lice from the interior of pinfeathers. This fact is not surprising because washing subjects the dead birds to prolonged, vigorous shaking in a detergent solution (see Materials and methods).

Our results call into question previous visual studies documenting apparent decreases in louse abundance associated with molt (Markov 1940; Blagoveshchensky 1959; Baum 1968; Marshall 1981). Some, if not all, of these studies may contain misleading data. The conventional wisdom that molt reduces ectoparasite abundance is not based solely on visual data, however; at least two studies of lice have used better methods to document reductions in louse abundance concurrent with molt. Chandra et al. (1990) fumigated freshly killed common mynas (*Acridotheres tristis*) and quantified their lice by ruffling the plumage. McGroarty and Dobson (1974) used body washing to quantify lice on dead house sparrows (*Passer domesticus*). Both of these studies showed a reduction in louse abundance in late summer, coincident with the bird's postnuptial molt. These seasonal decreases in abundance were probably real, but whether they are due to molt remains an open question, pending

experimental manipulations to establish molt as the cause of the decreases.

One factor other than molt that could easily explain reductions in louse abundance is dispersal of lice from parent to juvenile hosts. Lice typically disperse from parent birds to their offspring at the end of the breeding season (Eveleigh and Threlfall 1976; Clayton and Tompkins 1994; Lee and Clayton 1995). The result is a decrease in the abundance of lice on adult birds around the time of molt. Dispersal of lice to juveniles could also explain why fewer newly laid eggs are found on adult feathers near the end of the breeding season (Foster 1969).

Host physiological constraints may allow ectoparasites plenty of time to circumvent molt in most cases. For example, thermal insulation and aerodynamic efficiency are both known to be compromised in proportion to the number of feathers missing (Schieltz and Murphy 1997; Swaddle and Witter 1997). Energy is also required for every new feather being synthesized (Lindström et al. 1993). Recent work shows that feather quality is inversely proportional to the rate of molt (Dawson et al. 2000), suggesting that rapid molt is constrained. Like birds, most mammals also have a rather gradual molt (Murray and Nicholls 1965; Vaughan 1985). Even ectoparasites with limited powers of movement should be able to relocate to new feathers or hair, given the slow rate at which molt takes place.

The ability of ectoparasites to circumvent molt, regardless of its rate, presumes that they can detect and avoid feathers or hairs that are about to be lost. This assumption is supported in the case of quill mites (Acarina: Syringophilidae), which exit old feathers and enter the quills of new ones (Kethley 1971; Casto 1974). The cue used by the quill mites may be vibrations caused by the rocking of old feathers as they are pushed out of the follicle by emerging new feathers. Feather mites (Astigmata) also avoid feathers that are about to fall out during molt. Jovani and Serrano (2001) recently showed that feather mites are significantly less abundant on feathers that are about to be molted, compared to newer or older feathers. Our observations of lice using pinfeathers as refuges suggest that lice are at least capable of identifying new feathers that will not be lost. Some mammal lice are also capable of avoiding host molt. For example, the seal louse (*Lepidophthirus macrorhini*) burrows beneath the skin of the southern elephant seal (*Mirounga leonine*) in time to avoid being lost when the outer layer of skin is shed (Murray and Nicholls 1965). The coevolution of such mechanisms for avoiding molt are not surprising, given the close association of many ectoparasites with their hosts.

Molt may be a more important mechanism for jettisoning less mobile parasites, such as fungi and bacteria that live in plumage. Burtt and Ichida (1999) recently documented that feather-degrading bacteria show significant seasonal fluctuations, with the lowest infestations in the autumn. It would be interesting to conduct an experiment testing whether feather molt causes these seasonal reductions in plumage bacteria.

Molt may be far less gradual and regular in some cases. A handful of studies (reviewed in Taylor 1981) suggest that birds may be capable of adventitious molt in response to parasites such as quill lice. Adventitious molt would serve a similar function to premature leaf abscissions that reduce the abundance of herbivorous insects on some trees. Several studies have shown that leaf abscission reduces infestations of leaf miners and other endophytic and sessile insects (reviewed in Stiling et al. 1991). For example, Williams and Whitham (1986) showed that cottonwood trees (*Populus* spp.) can reduce gall aphid (*Pemphigus* spp.) populations by up to 50% by selectively dropping infested leaves. Work to determine whether adventitious molt really occurs, and its impact on ectoparasites, would be useful.

In the future, it would also be worthwhile repeating our experiment with two modifications. First, spatial pseudoreplication could be eliminated by distributing the experimental and control birds among several animal rooms. Although the two rooms we used provided uniform conditions, the use of several rooms would be more conservative. Second, it would be interesting to repeat our experiment using birds with normal preening ability, rather than bitted birds. We used bitted birds to eliminate the possibility that molt reduces ectoparasites indirectly through an increase in preening caused by irritated skin (Potter and Hauser 1974). Our results show that molt has no direct effect on ectoparasites. Although we think that an indirect preening-mediated effect is unlikely, it would be relatively easy to explicitly test for this possibility.

In summary, we showed that feather molt has no effect on the louse loads of captive feral pigeons. In light of our results, we argue that it is necessary to reinterpret the conclusions of previous investigations that were based on observational data. Our methods could easily be adopted to test the impact of molt in other bird species, mammals, and reptiles. Shedding of hair by mammals is said to reduce ectoparasites (Marshall 1981; Kim 1985; Lehane 1991). However, the supporting data for this assertion were gathered using visual methods (e.g., Murray 1957). As with birds, mammal molt can be triggered by altering photoperiod (Basset et al. 1944; Duby and Travis 1972), and body washing can be used to quantify the impact of molt on mammal ectoparasites (Henry and McKeever 1971). A rigorous experimental test of the impact of molt on mammal ectoparasites should thus be feasible.

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