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OCCURRENCE OF FEATHER-DEGRADING BACILLI IN THE PLUMAGE OF BIRDS

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ABSTRACT.—We sampled bacteria from the plumage of 1,588 individuals of 83 species of birds. Feather-degrading bacteria, those able to extract energy and nutrients by breaking up β-keratin, were isolated from 134 individuals in 32 species. Nine of 11 samples of feather-degrading (keratinolytic) bacteria were identified as *Bacillus licheniformis*, one as *B. pumilus*, and one as a *Bacillus* of undetermined species. A strong correlation between occurrence of keratinolytic bacilli and the number of birds sampled per species suggests that feather-degrading bacilli are widespread among birds. The bacillus occurred on 6.7 to 10.7% of birds and showed little annual variation. The incidence of birds with feather-degrading bacilli was highest in late fall and winter and lowest in early spring and late summer. The bacilli occurred most frequently on the venter and less commonly on the dorsum and tail. They occurred most frequently on ground-foraging species and least frequently on aerial-foraging species. Regardless of avian species, time of year, or area of the bird from which the bacilli were isolated, the rate at which bacilli degraded feathers was similar. Because bacilli are active only when conditions are warm and humid, we suggest that they degrade feathers during the summer when the bird becomes wet, for example during thunderstorms. Such feather degradation may contribute to the deterioration of feathers and be a selective force in the evolution and timing of molt. *Received 6 October 1997, accepted 29 July 1998.*

IN 1990, WILLIAMS AND COLLEAGUES (Williams et al. 1990) isolated a feather-degrading bacterium (*Bacillus licheniformis*) from a biodigester containing poultry waste. *Bacillus licheniformis* occurs in soil (Wood 1995), where it may help explain decomposition of molted feathers, but its potential occurrence on the plumage of birds raises important questions about its effect on feathers still on the bird.

Feathers contain β-pleated sheets of keratin twisted into microfibrils (Pauling and Corey 1951a, b; Brush 1978) and are unusually resistant to biological degradation (Goddard and Michaelis 1934, Parry et al. 1977, Lin et al. 1992). Prior to 1990, a few species of fungi (Pugh 1964, 1965; Hubálek 1976, 1978) and a single bacterium, *Streptomyces fradiae* (Noval and Nickerson 1959), were known to degrade feathers. These keratinolytic microorganisms occur in the soil (Pugh 1964). Some of the fungi also occur in the plumage of a few species of birds, whereas others occur on the bill, in the throat, or in old nests (Pugh 1964, 1965; Hubálek 1976, 1978). Unlike the fungi, keratinolytic bacteria were known only from soil and poultry compost (Shih 1993). Could such bacteria also occur in the plumage of living birds? If so, are the bacteria species or site specific as are the keratinolytic fungi? If feather-degrading bacteria occur in plumage, what is their potential effect on the birds that carry them? Here, we provide the first report on the occurrence of feather-degrading bacteria on the plumage of living, wild birds. We also examine the temporal and ecological variation in bacterial occurrence in birds and discuss the possible effect of such bacteria on plumage and avian biology.

METHODS

To look for feather-degrading bacteria in plumage and to determine its patterns of occurrence, we captured birds in mist nets and Potter traps from 18 May 1993 to 7 December 1996 at several locations in the Delaware Wildlife Refuge, Delaware, Ohio; at the Bohannan Forest Preserve and Kraus Wilderness Preserve of Ohio Wesleyan University, Delaware, Ohio; at the home of EHB, Ashley, Ohio; and at Manomet Observatory for Conservation Sciences, Manomet, Massachusetts. Canada Geese (*Branta canadensis*) were sampled at Killdeer Plains Wildlife Refuge, Harpster, Ohio. The plumage of Ruddy Ducks (*Oxyura jamaicensis*) was sampled at Delta Wildlife Refuge, Delta, Manitoba. Except for the Northern Waterthrush (*Seiurus noveboracensis*), which was sam-

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pled at EHB's home, all other water birds were sampled in Plymouth, Massachusetts.

We removed birds from the net or trap and rubbed a sterile Dacron-tipped applicator (Puritan) wetted with sterile saline (0.85% NaCl) on the dorsal feathers, another on the ventral feathers, and a third across the upper surface of the tail feathers. After exposure the applicators were replaced in their sterile envelopes and returned to the laboratory where they were removed from the envelopes, placed in sterile, individually labeled tubes of modified (pH 7.5, 7.5% NaCl) nutrient broth (Difco), and incubated at 50°C for seven days. If the media remained clear, bacteria were nonviable, and the tube was discarded. If the media became cloudy, bacteria were cultured by streaking a drop of media across a sterile plate of trypticase soy agar (TSA; Acumedia) and incubating the culture for 24 h at 35°C. This procedure enabled us to check the morphology of the bacterial colonies to be sure we were working with a single species and provided isolated colonies from which we selected one representative colony and transferred it to two slants of TSA. The slants were incubated for 24 h at 35°C. After growth, the cultures were stored at 4°C until further testing. We sent samples of our first 14 isolates to Five Star Laboratories, Milford, Connecticut, for species identification by cellular fatty acid analysis.

To test the bacterial isolates for feather degrading activity, we used secondary feathers of white leghorn chickens. We removed and discarded the distal 1 cm from the feather and placed the next 2 cm and the adjacent 2 cm in different test tubes. We added 10 mL of feather media (Williams et al. 1990) to each tube. Next, all tubes were sterilized at 121°C and 17 lbs pressure for 15 min. The bacterial isolates to be tested were removed from cold storage. We inoculated fresh TSA cultures. After 24 h, a loopful of bacteria was removed and suspended in sterile saline. The turbidity of the saline-bacterial suspension was adjusted to 0.5 MacFarland standard, which corresponds to about 150,000 cells/mL. Two drops of this suspension (ca. 0.1 mL) were placed in a test tube of feather media containing the feather. A replicate was prepared from the same suspension. Tubes were placed in a rack on a shaker that rotated at 175 rpm and incubated at 50°C. All tubes were checked daily for 14 days. We considered the feather to be degraded when only pieces 0.5 mm^2 or smaller remained.

Results

We sampled the plumage of 1,588 birds of 83 species for feather-degrading bacteria (see Appendix). We isolated 169 samples of bacteria, of which 134 (79.3%) degraded feathers. These results suggest that screening for feather-degrading bacteria by incubating samples in a modified nutrient broth at 50°C is an effective selection procedure for isolating salt tolerant, thermophilic bacteria. However, the technique does not identify the species of bacteria.

Identification of feather-degrading bacteria.—Of the 14 isolates sent to Five Star Laboratories, 9 were *Bacillus licheniformis*, 2 were *B. pumilus*, 1 was *B. subtilis*, and 2 were gram-positive, endospore-forming, rod-shaped bacteria that could not be identified further. All nine samples of *B. licheniformis* were able to degrade feathers, whereas the one sample of *B. subtilis* was unable to do so. One of the two samples of *B. pumilus* degraded feathers. Similarly, only one of the two samples of gram-positive, endospore-forming, rod-shaped bacteria degraded feathers. *Bacillus licheniformis* is gram positive, forms endospores, and is rod-shaped; the feather-degrading unknown bacterium may be *B. licheniformis*. Given this uncertainty, we conclude that 82 to 91% of the bacteria from avian plumage that grew under our culture conditions and degraded feathers were *B. licheniformis*, but that closely related species, for example *B. pumilus*, may also degrade feathers. Because we could not unequivocally identify each bacterial isolate, but all belong to the genus *Bacillus* morphological group I (Parry et al. 1983), we refer to them as feather-degrading bacilli throughout the remainder of the paper.

Temporal variation.—The plumage of birds is not a constant environment for microorganisms. Feathers are replaced once or twice a year in the species we sampled. Temperature varies within the plumage and is influenced by seasonal differences, whether the bird is a resident or a migrant. Moisture, another important component of the plumage microclimate, varies seasonally. To learn how such seasonal variation might affect feather-degrading bacilli, we looked at temporal variation in occurrence of the bacilli on the feathers of birds.

We sampled birds from forest, marsh, and old field (e.g. mixed grasses, with patches of brush and small trees) habitats, but 1,356 of the 1,588 birds we sampled were captured at three old field sites near Delaware and Ashley, Ohio. To control for possible habitat effects, the following analysis is limited to those birds captured in old field habitat.

The annual proportion of birds carrying feather-degrading bacilli varied nonsignificantly ($\chi^2 = 4.40$, df = 2, $0.25 > P > 0.1$) from a low of 6.7% (36 with *B. licheniformis* of 419 birds

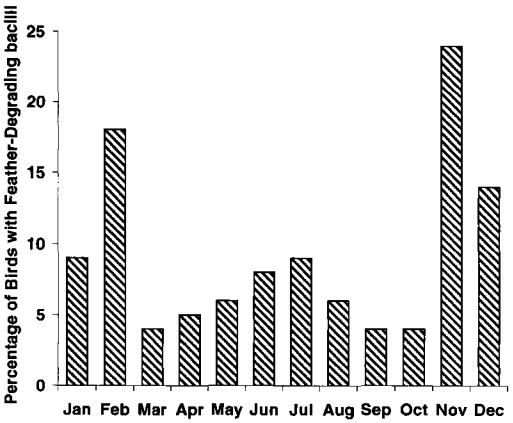

FIG. 1. Percentage of birds with feather-degrading bacilli plotted by month.

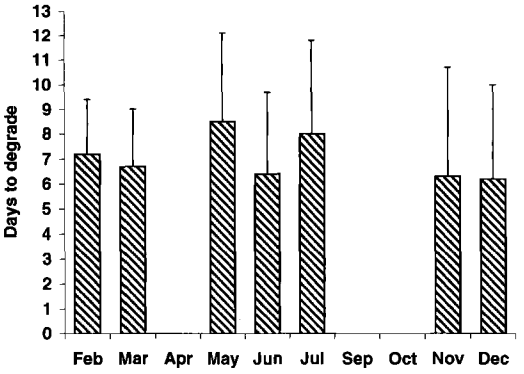

FIG. 2. Number of days required to degrade a 2-cm piece of feather as a function of the month in which bacilli were isolated.

sampled) in 1994 to a high of 10.7% (51/477) in 1996, with 1993 (7.4%, 25/285) and 1995 (9.4%, 32/341) intermediate. We obtained replicable measurements of the number of days required to degrade a feather for 56 isolates from 1993 and 1994. The number varied from 3 to 14 or more days, but the variation was unrelated to the year in which the bacilli were isolated ($t = -1.76$, df = 50, $P = 0.084$). These results enabled us to combine data from different years in the following analyses.

The proportion of birds with feather-degrading bacilli in their plumage differed significantly ($\chi^2 = 40.00$, df = 11, $P < 0.001$) from month to month (Fig. 1). The incidence of such bacilli was highest in the late fall (24% in November) and winter (18% in February), dropped to 4% in early spring, rose gradually to 9% in July, and dropped back to 4% in September and October before increasing abruptly in November (Fig. 1). No comparable pattern existed ($F = 0.51$, df = 6 and 49, $P = 0.51$) in the number of days isolates from different months required to degrade feathers (Fig. 2). Estimates for April, September, and October were omitted from the degradation analysis because the number of bacterial isolates was few, and we were unable to replicate our measures of the number of days to degrade a feather. The number of birds sampled varied from 25 in January to 252 in July; however, the monthly differences in sample size were not a significant determinant ($r = -0.189$, $P = 0.56$) of the monthly percentage of captured birds with feather-degrading bacilli.

Seasonal differences in the incidence of feather-degrading bacilli may result from differences in the avian species that comprise our monthly samples. Many species such as the Gray Catbird (*Dumatella carolinensis*) that were common in our summer samples were absent from our late fall and winter samples. Similarly, migrants and winter residents occurred in some samples but not in others. Among permanent residents, only House Sparrows (*Passer domesticus*) were caught in sufficiently large numbers with a sufficiently high incidence of feather-degrading bacilli to allow us to test for seasonality of bacterial occurrence in a single species (Fig. 3). Some monthly samples had to

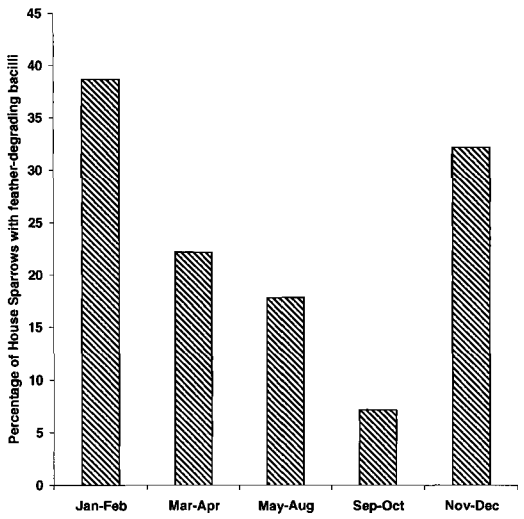

FIG. 3. Seasonal percentage of House Sparrows with feather-degrading bacilli.

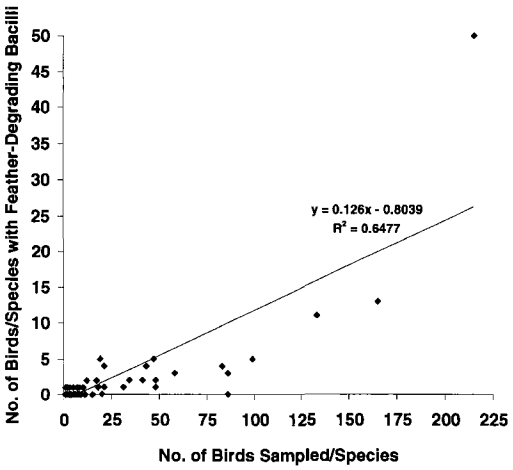

FIG. 4. Number of birds with feather-degrading bacilli plotted as a function of the number of birds sampled per species.

be combined to obtain large enough expected values for Chi-square analysis. The seasonal variation shown by House Sparrows (Fig. 3) was nonrandom ($\chi^2 = 10.07$, df = 4, $0.05 > P > 0.025$) and was similar to that shown by our multispecies sample (Fig. 1); i.e. the incidence of feather-degrading bacilli was highest in late fall and winter, intermediate in spring and summer, and lowest in September and October. Furthermore, when House Sparrows were removed from the multispecies analysis and some months were combined to obtain adequate expected values, monthly differences in the occurrence of feather-degrading bacilli remained nonrandom ($\chi^2 = 14.27$, df = 7, $0.05 > P > 0.01$). Monthly differences in the occurrence of the bacilli were not a product of sampling. They were not driven by a single, abundant, resident avian species nor by monthly differences in the species composition of our samples.

In summary, the incidence of feather-degrading bacilli in the plumage of eastern North American birds varied with the time of year, but not among years. Furthermore, the amount of time bacilli required to degrade feathers varied from 3 to 14 or more days, but the mean and variation in time required were similar from year to year and month to month.

Topographical variation.—Although feather-degrading bacilli occurred among the ventral, dorsal, and tail feathers, they were isolated more often ($\chi^2 = 10.2$, df = 2, $0.01 > P > 0.005$) from the venter (76 of 169 total isolates) than from the dorsum (51 of 169) or tail (42 of 169). However, the number of days required to degrade a feather did not vary ($F = 0.29$, df = 2 and 47, $P = 0.75$) with the area of the body from which the bacilli were isolated.

TABLE 1. Incidence of feather-degrading bacilli among avian species in which 70 or more individuals were sampled.

Species	*n*	Individuals with bacilli (%)
Gray Catbird	165	8
Northern Cardinal	99	5
American Tree Sparrow	86	0
Song Sparrow	133	8
House Finch	83	5
American Goldfinch	89	3
House Sparrow	215	23

Ecological variation.—Of the 83 species of birds sampled, 32 carried feather-degrading bacilli. However, the number of individuals sampled per species varied from 1 to 215, and our discovery of feather-degrading bacilli in the plumage of a species was significantly correlated with the number of individuals sampled ($r = 0.80$, $P < 0.001$; Fig. 4). Indeed, sample size accounted for 64% of the variation among species of birds in the occurrence of feather-degrading bacilli. Furthermore, the regression equation:

$$\text{birds per species with feather-degrading bacilli} = 0.126\ (\text{birds per species}) - 0.804 \quad (1)$$

predicts that we would need to sample an average of 14 individuals per species to find one individual with feather-degrading bacilli. In contrast to the strong correlation between the number of birds with feather-degrading bacilli per species and the number of birds sampled per species, the percentage of individuals per species with feather-degrading bacilli was independent of sample size ($r = 0.00$, $P > 0.9$).

Sample size accounted for a large proportion of the difference among species, but substantial differences remained even when sample size was controlled. Among those species represented by 70 or more sampled individuals (Table 1), the incidence of feather-degrading bacilli was significantly nonrandom ($\chi^2 = 48.32$, df = 6, $P < 0.001$). American Tree Sparrows (*Spizella arborea*) had an unusually low incidence,

TABLE 2. Incidence of birds with feather-degrading bacilli and mean number of days to degrade a feather by bacilli isolated from birds of different foraging guilds.

Foraging guild	No. of birds sampled	% of birds with bacteria	No. of isolates tested	No. of days to degrade feather ($\bar{x} \pm$ SD)
Aerial	83	2.4	2	5.5 ± 5.0
Bark-probing	90	3.3	1	14
Foliage-gleaning	296	4.7	17	7.8 ± 4.2
Water	125	8.0	1	5
Ground	993	10.7	29	6.4 ± 2.6

whereas House Sparrows had an unusually high incidence of feather-degrading bacilli.

These differences suggest that behavior and ecology affect the occurrence of feather-degrading bacilli among species. To address this possibility, we grouped species based on their foraging behavior and habitat (Appendix) as described in the species accounts edited by Bent (1919–1968) and Poole et al. (1992–1998). The incidence of feather-degrading bacilli differed significantly ($\chi^2 = 16.03$, df = 4, $P < 0.001$) among groups (Table 2), with aerial insectivores having the lowest incidence of feather-degrading bacilli, bark-probers and foliage-gleaners having an intermediate incidence, and water birds and ground-foragers having the highest incidence. The number of days to degrade a feather did not vary ($F = 1.15$, df = 2 and 46, $P = 0.325$) with foraging behavior or habitat of the species from which the bacilli were collected (Table 2).

DISCUSSION

The progressive deterioration of feathers must be the fundamental selective force acting on the evolution of molt. Pyle (1997) has described such deterioration among the criteria used in age determination in birds. Physical causes of deterioration, such as abrasion and ultraviolet irradiation, have received observational (Averill 1923, Bergmann 1982) and experimental (Burtt 1986, Bonser 1995) study. Microorganisms within the plumage have received scant attention, but they may be an important biological cause of deterioration. We explored the potential role of feather-degrading bacilli in the ecology of the plumage.

Keratinolytic microorganisms.—Feather-degrading bacilli were present in the plumage of 6.7 to 10.7% of the birds we examined, and 82 to 91% of the bacilli were *B. licheniformis.* The only other keratinolytic bacillus that we isolated from plumage, *B. pumilus,* exhibited minimal feather-degrading activity. Two other keratinolytic bacteria are known, *Streptomyces fradiae* (Kunert 1989) and *S. pactum* (Böckle et al. 1995). They are not known to occur in the plumage of wild birds, and we did not isolate them with our techniques.

In addition to bacilli, 13 species of keratinolytic fungi have been identified (Hubálek 1976, Kunert 1989). *Aphanoascus terreus, Arthroderma tuberculatum, A. ciferrii, A. curreyi, A. quadrifidum, Ctenomyces serratus,* and *Chrysosporium tropicum* have been isolated from the plumage of birds (Pugh 1964,1965; Hubálek 1976, 1978). *Aphanoascus fulvescens* and *Chrysosporium keratinophilum* have been isolated from old nests (Hubálek 1978). The remaining species, *Arthroderma multifidum, A. cuniculi, Ctenomyces evolceanui,* and *Microsporum gypseum* are known to degrade keratin (Hubálek 1976, Kunert 1989), but their association with birds is unknown. Also unknown is the potential interaction among keratinolytic fungi, such as *Chrysosporium* sp., which produce the antibiotic chryscandin (Yamashita et al. 1984), and keratinolytic bacteria, such as *Streptomyces fradiae,* which produce neomycin (Chandramohan and Nair 1992).

Temporal variation.—We can only speculate on reasons for the seasonal fluctuations of feather-degrading bacteria in avian plumage. Both of the species we identified, *B. licheniformis* and *B. pumilus,* form spores that enable them to survive long periods of unfavorable conditions. The high incidence of feather-degrading bacilli in avian plumage during winter may reflect a reduction in maintenance behavior that would remove spores from the feathers. No data are available on seasonal changes in the frequency of bathing or preening, but in cold climates the freezing of shallow, standing water would seem to reduce the opportunities for bathing by most birds. Whether birds can remove bacterial spores during bathing or preening is unknown. The lower incidence of feather-degrading bacilli in the late spring and summer could be due to increased maintenance behavior, but it could also be due to increased exposure to ultraviolet radiation, which is known to kill both vegetative bacterial cells and spores (Madigan et al. 1997). The minimal incidence of feather-degrading bacilli in

March, September, and October may result from disruption of bacterial populations following prealternate molt in late February and March and prebasic molt in late July and August. Unlike *B. licheniformis*, the keratinolytic fungus found in the plumage of birds shows no seasonal change in its occurrence (Pugh 1965).

Topographical variation.—Feather-degrading bacilli occur on the dorsum, venter, and upper surface of the tail of birds. We also isolated a few samples from the wings, although these were not sampled systematically. We conclude that the bacilli can occur anywhere in the plumage, which agrees well with the colonization of feathers by airborne spores. Although generally distributed in the plumage, feather-degrading bacilli occur most often on feathers of the venter. Bacilli are soil bacteria (Wood 1995), and to the extent that colonization of the plumage depends on direct contact with vegetative cells, the ventral feathers would be the most likely to contact soil. Furthermore, damp conditions favor bacterial growth, and the ventral feathers may be wet more often and longer than the dorsal feathers because of their frequent contact with wet vegetation (e.g. leaves covered with dew) and their limited exposure to the drying effect of direct sunlight. No comparable data exist for topographical distribution of keratinolytic fungi.

Ecological variation.—Sample size accounts for 64% of the variation among species in the number of individuals with feather-degrading bacilli in their plumage. Based on the strength of the correlation, we predict that such bacilli will be found in all species of birds that have been adequately sampled. Based on equation 1, a sample of 14 to 30 birds should include 1 to 2 individuals with feather-degrading bacilli. Indeed, such bacilli were isolated from every avian species except the American Tree Sparrow in which we sampled 30 or more individuals.

The percentage of individuals with bacilli also depends on avian behavioral ecology. Birds that catch insects in the air, those that glean insects from foliage, and those that probe bark for insects have a lower incidence of feather-degrading bacilli than water birds, which have an 8% incidence of the bacilli. Birds that forage on the ground have the highest incidence of feather-degrading bacilli (10.7% of all individuals sampled). The ecological pattern of incidence supports the conclusion, drawn above, that colonization of the plumage is through contact with bacilli in the soil and secondarily through airborne spores. Additionally, the plumage of birds that forage in water or on the ground is probably wet more often than the plumage of aerial insectivores. Wet plumage should be a more favorable habitat for *B. licheniformis* than dry plumage and more likely to allow successful colonization of the plumage of water birds and those foraging on the ground.

The ecological relationships between birds and feather-degrading fungi are poorly studied, but they appear to be similar to those for birds and feather-degrading bacilli. Among 470 European birds representing 41 species (Pugh 1965), ground-foraging species had a much higher incidence of keratinolytic fungi (*Arthroderma curreyi, A. quadrifidum, Chrysosporium* spp. and *Ctenomyces serratus*) in their plumage than did foliage-gleaning insectivores. Hubálek (1976) examined 502 birds and 367 nests of 90 European species and found that *Arthroderma curreyi, A. quadrifidum,* and *Ctenomyces serratus* were most frequent on the plumage of polyphagous, ground-foraging birds, whereas *Chrysosporium tropicum* was most frequent on the plumage and in the nests of birds that live in aquatic or forest habitats. Keratinolytic microorganisms occur most frequently in the plumage of ground-foraging birds and less frequently on species that forage above the ground. The latter species pick up the microorganisms either through their infrequent contact with the ground (e.g. when gathering nest material or dust bathing) or through contact with the aerial spores of bacilli and fungi.

Could the occurrence of feather-degrading bacilli in the plumage of birds affect the bird? The simple answer is that we do not know. We know that only vegetative cells can degrade β-keratin of feathers, vegetative cells require a warm and moist environment, and feathers typically provide a warm but dry environment. However, suppose that the plumage is wetted by dew or thunderstorm and remains wet for a couple hours. That is sufficient time for the *Bacillus* to emerge from its spore, produce its keratin-degrading enzyme, grow, divide, and, as the feather dries out, return to its spore state and await the next wetting. The effect of repeated episodes of enzymatic action would be to weaken the keratin in the cortex of the feather, thus reducing the feather's ability to withstand damage from airborne particles and col-

lisions with solid objects (e.g. vegetation). The result would be disintegration of the feather. The scenario outlined above yields two predictions: (1) wear of the feathers should be most rapid during the summer when warm temperatures and frequent rain or dew provide opportunities for bacterial growth within damp plumage; and (2) molt not only replaces weakened feathers, but also rids the plumage of the bacilli adhering to the worn feathers.

Although we have no quantitative data on the first prediction, our impression is that abrasion of feathers is much more rapid during the summer than during the winter and that feathers are more likely to break during the summer than the winter. Our data on the monthly incidence of birds with feather-degrading bacilli show that the proportion declines dramatically in March and again in September and October following the prealternate and prebasic molts. Such temporal variation suggests that bacilli contribute to the evolution of molt in birds. With so little known about the microorganisms that inhabit plumage, this possibility is intriguing, but much remains to be learned about how bacteria and fungi interact with each other and with feathers before we can fully evaluate their influence on plumage and, ultimately, on the biology of birds.

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APPENDIX. Incidence of feather-degrading bacteria among bird species listed taxonomically by foraging guild (centered in bold).

Species	*n*	No. with bacteria
Aerial		
Eastern Wood-Pewee (*Contopus virens*)	5	0
Acadian Flycatcher (*Empidonax virescens*)	11	0
Willow Flycatcher (*Empidonax traillii*)	48	2
Willow or Alder Flycatcher (*Empidonax* spp.)	1	0
Empidonax flycatcher (*Empidonax* spp.)	1	0
Eastern Phoebe (*Sayornis phoebe*)	1	0
Great Crested Flycatcher (*Myiarchus crinitus*)	4	0
Eastern Kingbird (*Tyrannus tyrannus*)	1	0
Tree Swallow (*Tachycineta bicolor*)	8	0
Northern Rough-winged Swallow (*Stelgdopteryx ruficollis*)	2	0
Bank Swallow (*Riparia riparia*)	1	0
Subtotal	83	2
Foliage-gleaning		
Ruby-throated Hummingbird (*Archilochus colubris*)	6	0
House Wren (*Troglodytes aedon*)	15	0
Carolina Wren (*Thryothorus ludovicianus*)	1	0
Ruby-crowned Kinglet (*Regulus calendula*)	6	0
Blue-gray Gnatcatcher (*Polioptila caerulea*)	2	0
Brown Thrasher (*Toxostoma rufum*)	2	1
Cedar Waxwing (*Bombycilla cedrorum*)	3	0
White-eyed Vireo (*Vireo griseus*)	6	0
Warbling Vireo (*Vireo gilvus*)	2	1
Red-eyed Vireo (*Vireo olivaceus*)	9	0
Yellow Warbler (*Dendroica petechia*)	43	4
Magnolia Warbler (*Dendroica magnolia*)	7	0
Yellow-rumped Warbler (*Dendroica coronata*)	6	0
American Redstart (*Setophaga ruticilla*)	1	0
Kentucky Warbler (*Oporornis formosus*)	2	0
Mourning Warbler (*Oporornis philadelphia*)	2	0
Common Yellowthroat (*Geothlypis trichas*)	47	1
Hooded Warbler (*Wilsonia citrina*)	3	0
Wilson's Warbler (*Wilsonia pusilla*)	1	0
Canada Warbler (*Wilsonia canadensis*)	1	0
Yellow-breasted Chat (*Icteria virens*)	4	0
Scarlet Tanager (*Piranga olivacea*)	1	0
Northern Cardinal (*Cardinalis cardinalis*)	99	5

APPENDIX. Continued.

Species	*n*	No. with bacteria
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	4	0
Red-winged Blackbird (*Agelaius phoeniceus*)	17	2
Baltimore Oriole (*Icterus galbula*)	4	0
Purple Finch (*Carpodacus purpureus*)	2	0
Subtotal	296	14
Bark-probing		
Red-bellied Woodpecker (*Melanerpes carolinus*)	1	0
Downy Woodpecker (*Picoides pubescens*)	15	0
Hairy Woodpecker (*Picoides villosus*)	5	0
Black-capped Chickadee (*Poecile atricapillus*)	3	0
Carolina Chickadee (*Poecile carolinensis*)	34	2
Tufted Titmouse (*Baeolophus bicolor*)	20	0
Red-breasted Nuthatch (*Sitta canadensis*)	1	0
White-breasted Nuthatch (*Sitta carolinensis*)	8	1
Brown Creeper (*Certhia americana*)	1	0
Bay-breasted Warbler (*Dendroica castanea*)	1	0
Black-and-white Warbler (*Mniotilta varia*)	1	0
Subtotal	90	3
Ground		
Mourning Dove (*Zenaida macroura*)	3	1
Eastern Bluebird (*Sialia sialis*)	6	0
Veery (*Catharus fuscescens*)	3	0
Swainson's Thrush (*Catharus ustulatus*)	2	0
Wood Thrush (*Hylocichla mustelina*)	3	0
American Robin (*Turdus migratorius*)	19	5
Gray Catbird (*Dumetella carolinensis*)	165	13
European Starling (*Sturnus vulgaris*)	1	1
Worm-eating Warbler (*Helmitheros vermivorus*)	1	0
Ovenbird (*Seiurus aurocapillus*)	7	1
Indigo Bunting (*Passerina cyanea*)	8	1
Dickcissel (*Spiza americana*)	1	1
Eastern Towhee (*Pipilo erythrophthalmus*)	2	0
American Tree Sparrow (*Spizella arborea*)	86	0
Chipping Sparrow (*Spizella passerina*)	3	0
Field Sparrow (*Spizella pusilla*)	12	2
Song Sparrow (*Melospiza melodia*)	133	11
Lincoln's Sparrow (*Melospiza lincolnii*)	2	0
Swamp Sparrow (*Melospiza georgiana*)	18	1
White-throated Sparrow (*Zonotrichia albicollis*)	58	3
White-crowned Sparrow (*Zonotrichia leucophrys*)	21	6
Dark-eyed Junco (*Junco hyemalis*)	41	2
Common Grackle (*Quiscalus quiscula*)	1	0
Brown-headed Cowbird (*Molothrus ater*)	10	1
House Finch (*Carpodacus mexicanus*)	83	4
American Goldfinch (*Carduelis tristis*)	89	3
House Sparrow (*Passer domesticus*)	215	50
Subtotal	993	106
Aquatic		
Snowy Egret (*Egretta thula*)	8	0
Black-crowned Night-Heron (*Nycticorax nycticorax*)	6	1
Canada Goose (*Branta canadensis*)	47	5
Ruddy Duck (*Oxyura jamaicensis*)	31	1
Herring Gull (*Larus argentatus*)	8	1
Common Tern (*Sterna hirundo*)	21	1
Least Tern (*Sterna antillarum*)	3	0
Northern Waterthrush (*Seiurus noveboracensis*)	1	1
Subtotal	125	10
Total	1,588	134