

FEATHER-BUSTING BACTERIA

DALE H. CLAYTON¹

Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA

I ONCE HAD A COLLEAGUE who delighted in the aphorism, which he proudly coined himself, "If it's too small to see with the naked eye, it ain't there." Sadly, this view may as well be true for ornithologists who study birds only through unaided eyes, binoculars, or spotting scopes. But birds can also be studied through conventional and electron microscopes. A microscopic perspective soon reveals that birds are flying petri dishes, teeming with microbes inside and out. For example, researchers have known for decades that the plumage harbors a diverse community of bacteria and fungi, including yeast (Hubálek 1994). Unfortunately, the influence of these creatures on the birds themselves has received little attention. Little attention, that is, until now. In a pioneering paper in this issue of *The Auk*, E. H. Burtt and J. M. Ichida (1999) show that plumage microbes could influence birds in important ways.

Burtt and Ichida provide evidence that many, if not most, species of birds have bacteria in their plumage, and that some of these bacteria can rapidly degrade feathers, at least under laboratory conditions. To test for the presence of bacteria, the authors rubbed sterile applicators over several feather tracts of freshly caught birds, then incubated these applicators in the lab. Viable samples were cultured on plates and the bacteria identified. In an ambitious survey of more than 1,500 individual birds, representing 83 species, Burtt and Ichida isolated bacteria from the feathers of nearly 10% of the individuals sampled. Because bacteria were probably undersampled at each step in the procedure, the incidence of 10% represents a minimum; the actual value could be much higher. Although feather-degrading bacteria were found in less than half of the species, the authors argue that this is an artifact of the small number of individuals sampled for many of the species (a common problem in parasitological field studies). Extrapolating from their data, they predict that most species of birds will have feather-degrading bacteria in their plumage.

Consistent with this prediction is the fact that 15 of the 16 most heavily sampled species (>30 individuals) had feather-degrading bacteria.

These results, although interesting, perhaps are not surprising. After all, bacteria are abundant on most animals; humans have up to several million of them per square centimeter of skin (Andrews 1977). The more striking components of Burtt and Ichida's paper are the results of *in vitro* experiments they carried out to test the effect of bacteria on feathers. The authors prepared test-tube suspensions containing small pieces (2 cm long) of domestic chicken feathers. They inoculated each suspension with bacteria from one of their field samples ($n = 169$), then checked them daily for two weeks. Within a few days, feathers in about 80% of the tubes were degraded into pieces less than 0.5 mm in length. These results show clearly that bacteria collected from wild birds can cause extensive damage to feathers *in vitro*. The damage is caused by one or more keratin-degrading enzymes released by vegetative bacterial cells.

Of course, *in vitro* experiments may overestimate the potential for bacterial damage under natural conditions. A pressing question, raised by the authors themselves, is whether the plumage of wild birds is humid enough for sustained bacterial growth and the accompanying enzymatic action. Another question is whether domestic chicken feathers, such as those used in the degradation experiments, might be more vulnerable to bacterial action than the feathers of wild birds. This could be the case if feathers have antibacterial properties (see below) that are lost under conditions of relaxed natural selection. Additional experimental work is needed to assess the effect of bacteria under more natural conditions.

Assuming that wild birds are vulnerable to some level of bacterial damage, two fitness consequences could result. First, the insulative efficiency of the plumage could be hampered, causing thermoregulatory stress and a consequent reduction in body mass and survival. This chain of events has been well documented in the case of damage to plumage by feather-

¹ E-mail: clayton@biology.utah.edu

feeding lice (Booth et al. 1993, Clayton et al. 1999). A second fitness consequence of feather damage might be a reduction in aerodynamic efficiency. Bacterial damage could interrupt the airflow over the surface of the plumage of a flying bird, particularly given that bacteria are abundant on distal regions of the feathers (Muza et al. 1999). Furthermore, bacteria could weaken feathers, leading to increased breakage that would compound the thermoregulatory and aerodynamic problems just described.

Assuming that bacteria reduce avian fitness under natural conditions, selection should favor the evolution of antibacterial defenses. It is conceivable, for example, that the chemical or physical composition of feathers plays a role in defense, just as the composition of leaves is important for defense against plant pathogens (Fritz and Simms 1992). Seasonal as well as facultative shedding of leaves can help rid plants of parasites (Williams and Whitham 1986). Molt may play a similar role in helping birds to rid themselves of bacteria. Burt and Ichida (1999) recorded a drop in the incidence of bacteria in March and September, possibly caused by the prealternate and prebasic molts. Experimental manipulation of molt, independent of other factors, would help to determine its effect on bacterial populations.

Unlike plants, birds have dynamic behavior that is a first line of defense against parasites. Preening and other forms of grooming are critical for keeping feather lice and other arthropods in check (Hart 1997). Experimental manipulation of preening could be used to determine its potential influence on bacteria and other microbes. Other behavior such as anting, dusting, sunning, and insertion of green vegetation in nests also might defend against bacteria. The most relevant evidence so far is work by Clark and Mason (1985) showing that plants inserted in the nest by European Starlings (*Sturnus vulgaris*) inhibit the growth of bacteria *in vitro*.

Anting behavior, long postulated to control ectoparasites, may reduce bacteria by allowing birds to acquire antibiotic secretions from the metapleural glands of ants (Ehrlich et al. 1986). This is an intriguing possibility in light of recent unpublished data that clearly show anting has no effect on feather mites or lice (summarized in Clayton and Wolfe 1993, Hart 1997). Dusting and sunning also may play a role in

microbial defense by making the plumage too dry to support bacteria. Dusting desiccates plumage (Healy and Thomas 1973), and sunning increases feather temperature so dramatically (Moyer and Wagenbach 1995) that it must also have a desiccating effect.

Finally, bacteria in feathers could also be relevant to the process of parasite-mediated sexual selection, which has received considerable attention (Hillgarth and Wingfield 1997). Elaborate plumage might function as a revealing handicap in allowing females to scrutinize feathers of displaying males to check for microbial damage. Choice of a "clean" mate could be important, given that bacteria are transmitted vertically between parent birds and their offspring in the nest (E. H. Burt et al. unpubl. data).

Before careening into a speculative rut, it is important to reiterate that it will be *essential* to test for fitness consequences of bacteria under natural conditions. If bacteria have no effect on the fitness of wild birds, they cannot select for the evolution of antibacterial defense. What we really need now are carefully designed experiments that measure proximate and ultimate consequences of bacteria to birds in the field, similar to approaches taken in studies of arthropod ectoparasites (Brown and Brown 1986, Møller 1990, Clayton et al. 1999). We also need more sophisticated comparative analyses of survey data like those collected by Burt and Ichida. The recent outpouring of avian phylogenetic information (Mindell 1997) makes it feasible to carry out phylogenetically controlled analyses (Harvey and Pagel 1991) to test for morphological and ecological correlates of bacterial incidence. Similar work on other bird parasites shows that host body size and abundance are important determinants of parasite load (Poiani 1992, Gregory et al. 1996, Gregory 1997). Burt and Ichida suggest that ground and water birds have more bacteria than aerial or canopy birds because transmission of bacteria is enhanced near the ground or around water. But the jury is still out, pending more rigorous comparative analysis of the survey data. Data such as these are relatively easy to collect with simple, inexpensive techniques that are harmless to birds. This means that such data can be collected by researchers with limited resources, yet unlimited vision.

LITERATURE CITED

- ANDREWS, M. 1977. *The life that lives on man*. Taplinger Publishing, New York.
- BOOTH, D. T., D. H. CLAYTON, AND B. A. BLOCK. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proceedings of the Royal Society of London Series B* 253:125–129.
- BROWN, C. R., AND M. B. BROWN. 1986. Ectoparasites as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology* 67:1206–1218.
- BURTT, E. H., JR., AND J. M. ICHIDA. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. *Auk* 116:364–372.
- CLARK, L., AND J. R. MASON. 1985. Use of nest material as insecticidal and anti-pathogenic agents by the European Starling. *Oecologia* 67:169–176.
- CLAYTON, D. H., P. L. M. LEE, D. M. TOMPKINS, AND E. D. BRODIE III. 1999. Reciprocal natural selection on host-parasite phenotypes. *American Naturalist* 153: in press.
- CLAYTON, D. H., AND N. D. WOLFE. 1993. The adaptive significance of self-medication. *Trends in Ecology and Evolution* 8:60–63.
- EHRlich, P. R., S. DOBKIN, AND D. WHEYE. 1986. The adaptive significance of anting. *Auk* 103:835.
- FRITZ, R. S., AND E. L. SIMMS (Eds). 1992. *Plant resistance to herbivores and pathogens: Ecology, evolution, and genetics*. University of Chicago Press, Chicago.
- GREGORY, R. D. 1997. Comparative studies of host-parasite communities. Pages 198–211 in *Host-parasite evolution: General principles and avian models* (D. H. Clayton and J. Moore, Eds.). Oxford University Press, Oxford.
- GREGORY, R. D., A. E. KEYMER, AND P. H. HARVEY. 1996. Helminth parasite richness among vertebrates. *Biodiversity and Conservation* 5:985–997.
- HART, B. L. 1997. Behavioural defence. Pages 59–77 in *Host-parasite evolution: General principles and avian models* (D. H. Clayton and J. Moore, Eds.). Oxford University Press, Oxford.
- HARVEY, P. H., AND M. D. PAGEL. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.
- HEALY, W. M., AND J. W. THOMAS. 1973. Effects of dusting on plumage of Japanese Quail. *Wilson Bulletin* 85:442–448.
- HILLGARTH, N., AND J. C. WINGFIELD. 1997. Parasite-mediated sexual selection: Endocrine aspects. Pages 78–104 in *Host-parasite evolution: General principles and avian models* (D. H. Clayton and J. Moore, Eds.). Oxford University Press, Oxford.
- HUBÁLEK, Z. 1994. Pathogenic microorganisms associated with free-living birds (a review). *Prirodovedne Prace Ustavu Akademie Ved Ceske Republiky v Brne* 28:1–74.
- MINDELL, D. P. 1997. *Avian molecular evolution and systematics*. Academic Press, New York.
- MØLLER, A. P. 1990. Effects of parasitism by a haematophagous mite on reproduction in the Barn Swallow. *Ecology* 71:2345–2357.
- MOYER, B. R., AND G. E. WAGENBACH. 1995. Sunning by Black Noddies (*Anous minutus*) may kill chewing lice (*Quadriceps hopkinsi*). *Auk* 112: 1073–1077.
- MUZA, M. M., E. H. BURTT, JR., AND J. M. ICHIDA. 1999. Distribution of bacteria on the feathers of eastern North American birds. *Wilson Bulletin* 111: in press.
- POIANI, A. 1992. Ectoparasitism as a possible cost of social life: A comparative analysis using Australian passerines (Passeriformes). *Oecologia* 92: 429–441.
- WILLIAMS, A. G., AND T. G. WHITHAM. 1986. Premature leaf abscission: An induced plant defense against gall aphids. *Ecology* 67:1619–1627.