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OVERVIEW

FEATHERS AT A FINE SCALE

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IN 1668, ANTOINE von Leeuwenhoek improved the crude microscopes that were being produced in Europe to better study small biological objects (Madigan et al. 1997). Although von Leeuwenhoek's microscope revolutionized biology—giving credence to, among other things, the theory of the cell—the microscope's potential escaped the attention of most ornithologists. Since the late 19th and 20th centuries, a small group of researchers have used microscopes to study feathers (for historical reviews, see Fox 1976, Prum 1999); but it was only recently that a consideration of feathers (and the organisms that live on them) has been united with traditional studies of colors and structures on a macroscopic level. The result is a new appreciation of the importance of the bacterial flora of feathers and their potential to serve as a selective force that can affect the colors of feathers.

Microbes were isolated from feathers more than 40 years ago (e.g. Gierløff et al. 1961; Pugh and Evans 1970a, b), but feather bacteria went largely unstudied until Burt and Ichida (1999) isolated feather-degrading *Bacillus* spp. from the feathers of several species. Shawkey et al. (2003a) subsequently cultured 13 distinct isolates from the feathers of House Finches (*Carpodacus mexicanus*). More comprehensive surveys, using both culture-based and culture-independent methods (see Amann et al. 1995 for a review of those methods and their importance in detecting microbial diversity), have revealed even greater microbial diversity on feathers (M. D. Shawkey et al. unpubl. data). Although it is now clear that feathers are capable of harboring a diverse microflora, the ecological role(s) of that microflora remain largely a mystery. Goldstein et al. (2004) improves our understanding of these roles.

Using standard microbiological methods, they demonstrate that feather-degrading bacteria degrade unmelanized white feathers more quickly and completely than melanized black

feathers *in vitro*. Those data, along with those in Burt and Ichida (2004), suggest that melanin may protect feathers against bacterial degradation and that many patterns of melanin-based coloration might have evolved in response to bacterial infestation. Melanized feathers have previously been shown to be harder and more resistant to abrasion than unmelanized feathers (e.g. Burt 1979, 1986; Bonser 1995; but see Butler and Johnson 2004), but Goldstein et al. (2004) is the first study to explicitly demonstrate melanized feathers' enhanced resistance to bacterial degradation. Melanin-based plumage is used in social signaling (e.g. Rohwer and Rohwer 1978) and may also be involved in thermoregulation (Walsberg 1983) and crypsis (Wallace 1889, Zink and Remsen 1986). Goldstein et al. (2004) suggest that resistance to the degrading effects of bacteria is another important function of melanin, and that observation may have important implications for the evolution of plumage color.

Bacterial degradation of feathers may be an important factor in the evolution of clinal variation in melanin-based color and could be a selective agent responsible for melanic plumage morphs. Burt and Ichida (2004) suggest that the well-recognized tendency for vertebrates to be more darkly colored in humid than in arid environments (Gloger's rule) may be partially caused by the better growth conditions for microbes in moist habitats. Song Sparrows (*Melospiza melodia*) living in humid environments showed a consistent trend to have more feather-degrading *Bacillus licheniformis* in their plumage (Burt and Ichida 2004) than those from more arid environments. Moreover, under identical lab conditions, strains of *B. licheniformis* isolated from humid environments degraded feathers more quickly than those from arid environments. Although preliminary, those data suggest that birds in humid environments may be darker because of stronger selection pressure from more potent feather-degrading bacteria.

The work of Burt and colleagues provides a nice complement to recent work on the genetic basis of melanism in birds. Theron et al. (2001)

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showed that variation in the MC1R locus, a gene that codes for a receptor protein involved in melanin synthesis, is associated with the melanic plumage morph in Bananaquits (*Coereba flaveola*). A single-point mutation at that locus causes melanin to be deposited in all feathers, creating a virtually all-black morph. Those black morphs are found almost exclusively in forests where relative humidity is high, whereas yellow morphs are found in dry lowland habitats (Wunderle 1981a, b). Given the observations of Goldstein et al. (2004) and Burt et al. (2004), it seems possible that bacterial degradation in humid habitats explains the selective advantage of black morphs there, and hence the retention of the mutant MC1R gene. Mundy et al. (2004) show similar associations between the MC1R gene and melanic plumage morphs in Lesser Snow Geese (*Anser c. caerulescens*) and Parasitic Jaegers (*Stercorarius parasiticus*)—an association that Doucet et al. (2004) report in mainland and island populations of White-winged Fairy-wrens (*Malurus leucopterus*)—but the association between those morphs, habitat humidity, and bacterial degradation is less clear. Bacterial degradation is one of a host of potential selective factors acting on plumage. Among bird species that experience substantial variation in humidity across their range, however, a high percentage of them adhere to Gloger's rule (~94%; Zink and Remsen 1986), which suggests that bacterial degradation may be important in shaping avian coloration.

Of course, melanin deposition is but one means by which birds color their feathers. Carotenoid pigments are used by many birds to create bright red and yellow colors that tend to be involved in sexual signaling (reviewed in Hill 2002). Although the antioxidant properties of carotenoids are well known, their effects on feather structure and potential contribution to degradation resistance are not. Other than microstructural studies of feathers with structural and carotenoid green color (Dyck 1976, Prum et al. 1999), the tensile properties, resistance to degradation, and microstructure of feathers with carotenoid color have not been studied. Such studies would provide great insight into the costs and benefits of having brightly colored plumage.

Much more is known about the anatomy and physical properties of feathers with structurally based color (for a review, see Prum 1999), which also appears to be used in sexual signaling (Keyser and Hill 1999, Hunt et al.

1999, Siefferman and Hill 2004). Structural feather coloration is produced by one of at least six tissue types, with complex arrangement at the nanoscale (Prum 1999). There is clear potential for interactions between microbes and those microscopic feather structures. In Eastern Bluebirds (*Sialia sialis*), and likely other passerine birds with noniridescent purple and blue coloration, feather barbs produce color. Barbs have a central air-filled vacuole, a spongy medullary layer composed of a tightly arranged matrix of keratin and air pockets, and a keratin cortex (Shawkey et al. 2003b). The spongy layer, the object of most research, scatters light in such a way that it creates constructive interference with specific wavelengths of light, producing a brilliant color display. There is greater potential for bacterial interaction with the outer keratin cortex than with the spongy layer, and recent evidence suggests that the thickness of the keratin cortex has a significant effect on brightness (Shawkey et al. 2004). In Blue Tits (*Parus caeruleus*), brightness has been shown to increase throughout the breeding season (Örnborg et al. 2002). Perhaps, bacteria attach to and degrade the keratin cortex, contributing to an overall increase in brightness. Experimental application of feather-degrading bacteria to structurally colored feathers *in vitro* and *in vivo*, combined with spectrometry and electron microscope observation, could be used to test that hypothesis.

Other bird species, particularly those with iridescent color, use structural tissue in their barbules to create color (Prum 1999). Color of reflected light in those species is frequently caused by the layered arrangement of melanin granules beneath a thin keratin cortex (Prum 1999; but see Brink and van der Berg 2004). It is intriguing that color production in barbules, which are much thinner (Lucas and Stettenheim 1972) and hence more susceptible to wear than barbs, is dependent on melanin whereas color production in barbs is not. Indeed, even barbules on colored barbs tend to be heavily melanized. Perhaps, that melanization evolved partly as a defense against degradation, and only later became involved in production of bright color. That question could be addressed through phylogenetic analyses of the mechanisms of structural color.

The potential for new discoveries at the intersection between microbiology and ornithology is enormous. Goldstein et al. (2004), with a simple experiment, have opened up a realm of possibilities in the entirely new field

of evolutionary interactions between microbes and feather color. By using both microscopes and binoculars, we are likely to achieve a better understanding of the function and evolution of feather coloration.

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