1977. Marine fish communities, p. 451–492. *In* M. L. Merritt and R. G. Fuller [eds.], The environment of Amchitka Island, Alaska. TID-26712, National Technical Information Service, Springfield, VA.

WHITE, C. A., F.S.L. WILLIAMSON AND W. B. EMISON. 1977. Avifaunal investigations, p. 227–260. *In* M. L. Merritt and R. G. Fuller [eds.], The environment of Amchitka Island, Alaska. TID-26712, National Technical Information Service, Springfield, VA.

YOSHIDA, H., AND H. YAMAGUCHI. 1985. Distribution and feeding habits of the pelagic smooth lumpsucker, *Aptocyclus ventricosus* (Pallas), in the Aleutian Basin. Bull. Fac. Fish. Hokkaido Univ. 36(4):200–209.

The Condor 97:590–591

MELANIN AND THE ABRASION RESISTANCE OF FEATHERS[1]

RICHARD H. C. BONSER
School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, U.K.

Key words: Indentation hardness; feather keratin; melanin; abrasion; Willow Ptarmigan.

It has long been accepted that melanic feather keratin is more effective at resisting abrasive wear than non-melanic keratin (Averil 1923; Finnis 1959; Burtt 1979, 1986; Barrowclough and Sibley 1980; Bergman 1982; Lee and Grant 1986). The mechanical basis for this difference has yet to be determined. Voitkevich (1966) proposed that melanic keratin was less susceptible to wear as it is considerably thicker than non-melanic keratin. Differences in keratin thickness provide a reasonable explanation for the observed differences in wear resistance, however, the inclusion of granular fillers in polymers is known to increase their abrasion resistance (Lancaster 1973). As melanin is incorporated in feather keratin as granules (Filshie and Rogers 1962), it may function in this manner. Recently, Bonser and Witter (1993) found that in bills of the European Starling, *Sturnus vulgaris,* melanic keratin was significantly harder than non-melanic keratin. The wear resistance of a material is inversely proportional to its indentation hardness (Lipson 1967, Lancaster 1973, Barwell 1979). Thus, very hard materials wear less quickly than less hard ones. It is relatively easy to perform tests of indentation hardness, so this provides a very good method of determining the competence of a material to resist wear.

The maintenance of feathers is of vital importance to birds. Abrasion is an important mode of damage, and may initiate cracks in keratin that result in the fracture of feathers. This paper will quantify the differences in indentation hardness that are responsible for the differential abrasion resistance of melanic and non-melanic feather keratin.

MATERIALS AND METHODS

A primary remige was removed from each of twelve Willow Ptarmigan, *Lagopus lagopus* race *scoticus.* The birds had been stored frozen at −20°C since death. A 10 mm section of shaft was cut from each feather. The melanic dorsal, and non-melanic ventral surfaces of the shaft were separated, and the medullary foam scraped away from the keratin. Specimens were taken from opposing faces of the rachis at the same point along the rachis as it is known that substantial variation in material properties occurs along the rachis (Bonser and Purslow, in press). These specimens were glued to squares of perspex with cyanoacrylate adhesive. Vickers microhardness was determined using a Leitz "Wetzlar" miniload machine. The testing protocol followed that described by Bonser and Witter (1993). The indentor was allowed to remain on the specimen for 15 sec and the indentation measured after a further 45 sec. It is necessary to maintain rigorously these timings to prevent inaccuracies due to the viscoelastic creep of keratin. A load of 5 g was used in all tests. Ten indentations were made per specimen. Vickers hardness, *VHN* (kg mm^{-2}), is calculated using the formula

$$VHN = 1854P/d^2$$

where P is load in g, d is the diagonal length of the indentation in μm.

Paired *t*-test comparisons were performed on the pairs of data (melanic and non-melanic keratin) from each feather shaft.

RESULTS AND DISCUSSION

Melanic keratin from grouse primary feathers is significantly harder than non-melanic keratin ($T_{11} = 6.13$, $P < 0.001$). Mean Vickers hardness (SE) of the melanic sections was 14.63 kg mm^{-2} (0.96) and for the non-melanic sections, 10.51 kg mm^{-2} (0.44). Materials theory predicts that melanic keratin will sustain less wear than non-melanic keratin under equal abrasive con-

---

[1] Received 22 November 1994. Accepted 21 December 1994.

ditions. Although thicker keratin is more likely to resist wear than thin keratin (see Voitkevich 1966), the inclusion of keratin granules appears to increase the hardness of feather keratin by roughly 39%; since wear rate is inversely proportional to indentation hardness, non-melanic keratin would have to be 39% thicker than melanic keratin to resist the same amount of abrasion. Melanin may offer protection against abrasive wear at low metabolic cost.

Fracture. Burtt (1986) noted that melanism afforded a decreased likelihood of fracture of feather barbs and barbules. Scratches are necessary to initiate crack propagation that may result in failure by fracture. This is particularly important for materials subject to cyclical loading. Since feathers are loaded cyclically during flapping flight, it might be expected that feathers would be 'designed' to minimize the risk of fracture.

The energy that is available at the tip of a crack for its propagation is proportional to the square of the crack's depth, and consequently, the deeper the crack, the greater the risk of fracture (see Gordon 1978). There is a critical length over which cracks become self-propagating. This is known as the "critical Griffith length," l_g (m).

$$l_g = 2WE/\pi s^2$$

where s is the stress (Nm^{-2}), E is the Young's modulus (Nm^{-2}) and W is the work of fracture ($J\ m^{-2}$).

The volume of material removed by an abrasive particle under constant load is inversely proportional to hardness. Therefore hard materials will sustain less deep cracks as a result of abrasive wear so the harder melanic keratin would be less likely to develop cracks than non-melanic keratin. The probability of failure due to fracture would be considerably lower for melanic feather shafts. It is important to note that although the hardness of a material may affect crack initiation, there are no reasons to suppose that melanins will alter the work of fracture required to propagate such cracks.

It is possible that, in some instances at least, coloration may fulfill a mechanical role as well as intra- and inter-specific signalling. Since damage to feathers can not be corrected until moult, feathers should be as robust as economically possible. The costs incurred by melanin synthesis may substantially reduce the increases in metabolic cost of flight due to abrasion damage.

The author wishes to thank Dr. J.M.V. Rayner for his comments on drafts of this manuscript. The author was supported by a SERC research studentship and by a research grant awarded to Dr. J.M.V. Rayner by the Nuffield Foundation.

LITERATURE CITED

AVERIL, C. K. 1923. Black wing tips. Condor 25:57–59.

BARROWCLOUGH, G. F., AND F. C. SIBLEY. 1980. Feather pigmentation and abrasion-test of a hypothesis. Auk 97:881–883.

BARWELL, F. T. 1979. Bearing systems principles and practice. Oxford Univ. Press. Oxford, England.

BERGMAN, G. 1982. Why are the wings of *Larus f. fuscus* so dark? Ornis Fenn. 59:77–83.

BONSER, R.H.C., AND P. P. PURSLOW. In press. The Young's modulus of feather keratin. J. Exp. Biol.

BONSER, R.H.C., AND M. S. WITTER. 1993. Indentation hardness of the bill keratin of the European Starling, *Sturnus vulgaris.* Condor 95:736–738.

BURTT, E. H. 1979. Tips on wings and other things. *In* E. H. Burtt [ed.], The behavioral significance of color. Garland STPM Press, New York.

BURTT, E. H. 1986. An analysis of physical, physiological and optical aspects of avian coloration with emphasis on Wood-Warblers. Ornithol. Monographs 38:X + 1–126.

FINNIS, R. G. 1959. Aberrant juvenile blackbird *Turdus merula merula* Linnaeus. Bull. B.O.C. 79:152.

FILSHIE, B. K., AND G. E. ROGERS. 1962. An electron microscope study of the find structure of feather keratin. J. Cell Biol. 13:1–12.

GORDON, G. E. 1978. Structures. Penguin, Harmondsworth, U.K.

LANCASTER, J. K. 1973. Basic mechanisms of friction and wear of polymers. Plastics and Polymers 41: 297–306.

LEE, D. S., AND G. S. GRANT. 1986. An albino Greater Shearwater—feather abrasion and flight energetics. Wilson Bull. 98:488–490.

LIPSON, C. 1967. Wear considerations in design. Prentice-Hall, Englewood Cliffs, NJ.

VOITKEVICH, A. A. 1966. The feathers and plumage of birds. Sidgwick and Jackson, London.