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INDENTATION HARDNESS OF THE BILL KERATIN OF THE EUROPEAN STARLING[1]

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The European Starling, *Sturnus vulgaris,* is notable for the marked changes in bill coloration which occur through its annual cycle (e.g., Nichols 1945, Wydowski 1964, Feare 1984). From mid-winter through to the breeding season, the bill is pale or yellow. Following breeding, at the onset of molt, the bill becomes dark due to deposition of melanin granules (e.g., Witschi 1961, Filshie and Rogers 1962). For many species, it has been argued that changes in bill color may have been selected as sexual or social signals (e.g., Witschi 1961, Hardy 1974, Garson et al. 1980, Lawton and Lawton 1985). As an alternative, we propose that changes in bill coloration may have a mechanical function. It is well known that the presence of fillers affect the mechanical properties of polymers (see Ferry 1961). Furthermore, Averill (1923) noted that white areas of gull primary feather vanes wear more quickly than dark areas. Therefore, we hypothesize that the incorporation of melanin granules into bill keratin may increase wear resistance. Experimental studies of feather abrasion (e.g., Bergman 1982, Burtt 1986) have not considered how melanin affects the material properties of keratins. In this paper, we examine the indentation hardness of melanic and non-melanic bill keratin of the Starling. These measures have direct implications for wear resistance because it has been demonstrated previously that the indentation hardness of a material is inversely proportional to its wear rate (e.g., Lipson 1967, Lancaster 1973, Barwell 1979). That is, a hard material loses less volume than a less-hard material under the abrasive action of an equal force. This has been discussed mainly for metals (Lipson 1967, Barwell 1979), but also holds true for viscoelastic polymers (Lancaster 1973), such as keratin.

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The link between avian bill morphology and feeding ecology, in a between-species context, has long been acknowledged by ornithologists. More recently, there has been a growing appreciation of the changes in bill morphology which occur within individuals, often on a seasonal basis (e.g., Clancey 1948; Davis 1954; Hulscher 1985; Gosler 1987a, 1987b; Morton and Morton 1987; Matthysen 1989). The outer surface of the bill, the rhamphotheca, is a continuously growing structure in most birds (Stettenheim 1972), so bill morphology is determined by rates of both growth and wear. Within-individual changes in bill morphology have been viewed either as passive reflections of changes in dietary protein content (e.g., Morton and Morton 1987) or changes in abrasion (e.g., Davis 1954, Hulscher 1985, Matthysen 1989), or as an adaptive response to dietary shifts, though strategic adjustment of growth rate (e.g., Clancey 1948; Gosler 1987a, 1987b). In agreement with Gosler's (1987a) suggestion, Cuthill et al. (1992) and Witter and Cuthill (1992) demonstrated experimentally an additional mechanism through which adaptive changes in bill morphology may arise. They found that European Starlings, *Sturnus vulgaris,* are able to adjust strategically both bill-wiping frequency and choice of wiping substrate dependent upon the requirement to hone the bill. However, the extent to which the bill is abraded by, for example, bill-wiping is dependent upon the mechanical properties of the bill, in particular upon its ability to resist wear. We present here an analysis of the hardness of melanic and non-melanic bill keratin. We then discuss the implications of our results for trade-offs between wear resistance, growth rate, and plasticity.

METHOD

Hardness testing. Hardness testing is a rapid method of gauging the mechanical competence of a material. It has the advantage that small, irregularly shaped specimens can be tested. The procedure involves the application of a pyramidal indentor to the test piece under constant load. The dimensions of the indentation remaining after removal of the load are proportional to the depth to which the indentor has penetrated. However, with viscoelastic materials, such as keratin, one must be careful to eliminate the effects of creep after load removal, because the indentation will rapidly decrease in size for a short period of time, and will then remain at constant dimensions indefinitely. It is therefore necessary to define rigorously the loading conditions under which the tests are carried out.

PROCEDURE

The bills of ten birds were used for the hardness tests. Five individuals had melanic, black bill tips. The remaining birds had non-melanic, pale bill tips. All birds had been kept frozen at −20°C after death. Sections of the rhamphotheca, measuring approximately 1.5 × 5.0 mm, were cut just posterior to the bill tip. These sections were then bonded to squares of perspex, with the outer bill surface uppermost, using cyanoacrylate adhesive. The hardness tests were performed using a Leitz miniload microhardness testing machine. The procedure follows that of Hillerton et al. (1982). A load of 5 g was used in all tests. The indentor was applied for 15 sec, and a further 45 sec was allowed to elapse before the diagonals of the indentation were measured. This procedure was adopted to minimize discrepancies due to creep (see above). Ten such indentations were applied per specimen, all within 1 mm^2. Hardness (VHN) was calculated according to the formula:

$$\text{VHN} = 1854\ P/d^2\ (\text{kg mm}^{-2}),$$

where P is the load (g) and d is the mean length (μm) of the diagonals of indentation. The mean hardness, from the ten indentations performed on each section, was used in the analysis.

RESULTS AND DISCUSSION

In agreement with our hypothesis, melanic bill sections were significantly harder than non-melanic sections ($t_8 = 4.03$, $P = 0.0051$) (Fig. 1). This implies that melanic keratin would undergo less wear under similar abrasive regimes.

The levels of abrasion which Starlings experience in the wild will fluctuate due to diet composition and the substrate from which the food is obtained. Previously, it has been argued that bill morphology can be maintained under changing conditions of abrasion by varying growth rate and the degree of abrasion due to bill-wiping (e.g., Gosler 1987a, 1987b; Cuthill et al. 1992: Witter and Cuthill 1992). Here, we have identified a possible additional mechanism. Under conditions of increased abrasion, often experienced during the winter (e.g., Davis 1954, Matthysen 1989), the degree of wear experienced by the bill can be reduced by increasing the hardness of the rhamphotheca. As environmental abrasion increases, increasing bill hardness may be a less costly strategy, in terms of protein requirements, than increasing bill growth rate. The net benefit of incorporating melanin into the bill will, of course, also depend on the nature of any costs of melanin deposition, for example, due to the requirement to obtain necessary dietary precursors or because bill morphology can not be changed rapidly in the face of dietary

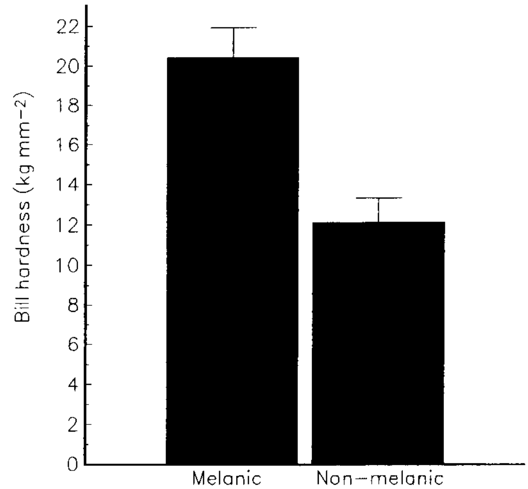

FIGURE 1. Mean (+SE) hardness for melanic and non-melanic bill sections.

shifts (c.f. Cuthill et al. 1992). It is unclear whether such putative costs can account for the loss of melanism during the breeding season when levels of environmental abrasion may be lower. An alternative interpretation may be that the cost of having a non-melanic bill (say, in terms of increased bill wear) is important in maintaining the honesty of a bill-color signal (c.f. Zahavi 1975, Grafen 1990).

Such changes in bill hardness are also expected to influence decisions regarding bill-wiping behavior because the wear per wipe would be less for a melanic bill. This may entail significant costs, including reduced awareness of surrounding stimuli and "lost opportunity" due to the time and energy expended performing the activity (Witter and Cuthill 1992). However, resulting changes in overall wiping frequency would also be predicted to depend on both growth rate and non-wiping abrasion, both of which may change in tandem with bill coloration. Clearly, this needs to be examined experimentally by simultaneously monitoring bill hardness, growth rate and wiping frequency under different abrasion regimes, as employed by Cuthill et al. (1992), in birds with melanic and non-melanic bills.

Changes in bill coloration are known to occur in a variety of species, usually due to the deposition of melanins or carotenoids (see Witschi 1961). Although the often conspicuous changes in coloration may serve as sexual or social signals (e.g., Witschi 1961, Hardy 1974, Garson et al. 1980, Lawton and Lawton 1985), the biomechanical consequences of the changes are rarely considered. We have shown that the deposition of melanin can result in increased bill hardness and this may have important implications for the maintenance of bill shape and, thus, foraging behavior. Our results also have important implications for studies which have attempted to quantify seasonal changes in environmental abrasion from patterns of bill wear (e.g., Matthysen 1989). Such studies implicitly assume that bill hardness does not vary over the period of measurement. Here, we have presented a technique by which this assumption can be directly tested.

Microhardness testing is a useful, non-destructive method of quantifying the functional characteristics of bill keratin. The greatest indenter penetration observed was 15.35 μm. Since the thickness of the keratinous layer is in the order of 3 mm, there is no danger of damaging the underlying bone. It seems likely that hardness testing can be applied to whole bills, if sufficiently well supported. As such, the technique may have relevance for examining museum specimens, or even anesthetized live birds, allowing within-individual changes to be quantified.

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