Feather Pigmentation and Abrasion: Test of a Hypothesis

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Explanation in ecology and evolutionary biology frequently is characterized by the discernment of pattern in the natural history of organisms, followed by the inference of cause to factors thought to be sufficiently important to have given rise to the pattern. Unfortunately, the process may end at this point because of difficulties in getting real organisms to adjust their behavior, size, shape, or color in such a manner as to yield control and experimental conditions and, hence, to lead to a test of the hypothesis. Laboratory experiments may lend support or raise doubts about the hypothesis, but the verification of the importance of the hypothesized factors in natural populations frequently rests on the observation of the results of natural experiments.

Recently, Burtt (1979) examined the relationship between feather coloration and wear due to abrasion. Earlier authors had mentioned anecdotal and qualitative observations about color and feather wear, for instance in the primaries of gulls (Averill 1923); Burtt, however, undertook a careful laboratory study of the abrasive effects of particles of silicon on the tail feathers of wood warblers. Based on the differential effects of this abrasion on feathers with and without melanin, along with the observed pattern of occurrence of melanic feathers among species of wood warblers, he concluded that the resistance to abrasion conferred on feathers by melanin was of sufficient importance that it should be considered an ecological function of the coloration. Nevertheless, the critical test of this hypothesis requires the observation of whether unpigmented feathers on a member of a natural population suffer significant wear due to the levels of abrasion normally encountered by a wild bird. Otherwise, one might conclude that Burtt's laboratory results were due to an unrealistically high particle flux. Recently, we happened upon a natural experiment that may help to elucidate this matter.

We collected a partial albino adult male Yellow-rumped Warbler (Dendroica coronata auduboni) in the Cascade Mountains of Washington on 10 July 1977 (Bell Museum Nat. Hist. No. 31921). The albinism was limited to the outer five primaries of the bird's left wing. Thus, primary feathers with and without melanin, on the right and left wings, were exposed, since the previous molt, to the same natural

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TABLE 1. Lengths and areas of pigmented and unpigmented primaries from a partial albino Yellow-rumped Warbler.

<table>
<thead>
<tr>
<th>Primary number</th>
<th>Left wing (albino)</th>
<th>Right wing (pigmented)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length (cm)</td>
<td>Area (cm²)</td>
</tr>
<tr>
<td>5</td>
<td>6.12</td>
<td>2.7</td>
</tr>
<tr>
<td>6</td>
<td>6.07</td>
<td>2.6</td>
</tr>
<tr>
<td>7</td>
<td>6.13</td>
<td>2.6</td>
</tr>
<tr>
<td>8</td>
<td>6.23</td>
<td>2.6</td>
</tr>
<tr>
<td>9</td>
<td>5.85</td>
<td>2.5</td>
</tr>
</tbody>
</table>

* Tip of this feather had been shot off.

environment. When the bird was collected the inner two primaries (Nos. 1 and 2) of both wings were in molt. This, in addition to what is known about molt in this species (Hubbard 1967), suggests that the primary feathers were approximately 11 months old and hence had been through nearly 1 year's exposure to abrasion. We measured flattened lengths of the primaries with dial calipers and surface areas with a planimeter (Table 1). The lengths and areas of the unpigmented feathers are significantly smaller than are the pigmented ones [paired t-tests: t = 7.09 (length) and 6.12 (area), df = 3, P < 0.01]. The differences in lengths of comparable primaries vary from 5% to 11%; differences in area are between 10% and 21%. Clearly, in the course of a year, melanin prevents an appreciable amount of wear on the primaries. This is in conformance with Burtt's thesis.

To evaluate the ecological relevance of the above findings, we investigated the effect that the differential wear has on flight energetics. We used Greenewalt's (1975) formula, as given by Schnell and Hellack (1979) in SI units, where the power required for flight was taken as:

\[ P = 6.76 \cdot 10^{-2} V^{2.7} S^{5.7} b^{0.5} + 460.52 M^{0.91}/V b^2. \]

P is the power input (watts), V is the magnitude of velocity (m/s), S is the surface area of the wings (m²), b is the wingspan (m), and M is the bird's mass (kg). For these energetic calculations, we used Poole's (1938) data for a subspecies of the Yellow-rumped Warbler (Dendroica c. coronata). For a pigmented (control) bird, mass was taken to be 0.0155 kg, surface area to be 0.0091 m², and wingspan to be 0.243 m. The velocity that minimized energy expenditure was calculated as follows: we took the partial derivative of the equation for P with respect to V, set it equal to zero, and solved for \( V_{opt} \). For the figures cited above, \( V_{opt} \) was 5.666 m/s; the corresponding value of P was 0.659 watts.

We calculated the power requirement of a theoretical albino warbler in the following way. We assumed primary and secondary feathers comprise 75% of the wing surface area. The outer primaries were assumed to contribute 50% to wingspan. These assumptions seem reasonable and are consistent with our measurements. Finally, we assumed that an albino bird would suffer the same percentage wear on its primaries and secondaries as did the bird we collected. In that case the average difference in primary length of 8.6% and the average difference in primary and secondary area of 16.0% would result in a decrease in wingspan of 4.3% and in wing surface area of 12.0%. \( V_{opt} \) for such a bird was computed; it was 5.966 m/s. The corresponding power requirement, P, was 0.683 watts. Consequently, the differential feather abrasion appears only to result in a 3.7% difference in power requirement.

It is conceivable that the reduction of wing surface area affects birds in some other way than this small increase in power requirement for sustained flight; for instance, it might result in a loss of maneuverability. Also, rapid wear might necessitate additional molts or reduce flexibility in molt timing. A crude estimate of the magnitude of the first effect is possible. The equation for power includes two terms, one of which is induced power (460.52 \( M^{0.91}/V b^2 \)). For normal flight this represents the power required to overcome the negative acceleration of gravity (Pennycuick 1969). If in maneuvering, however, the wings are used to create a force to overcome the bird's inertia, then this term suggests that the power required for such purposes will be proportional to \( b^{-2} \). The observed decrease in \( b \) of 4.3% due to abrasion suggests that about 9.2% more power would be required by a melanin-less individual to perform maneuvers similar to a normally pigmented individual.

We are left with something of an enigma. It was shown that Burtt was correct in that melanin significantly inhibits feather wear on a bird in a natural environment. Thus, one question raised by Burtt's study has been answered. A new question has arisen, however, in that it is not clear how significant the resulting 4% to 9% aerodynamical power savings is to a bird. For example, during molt Yellow-rumped Warblers may lose up to 30% of their wing surface area (Hubbard 1967). Alternatively,
plausible arguments can be made that, in aerial maneuvering, 9% may make a significant difference to a bird being chased by an accipiter, or to a sallying specialist like the Yellow-rumped Warbler. The estimates of the power differentials were for feathers with 11 months of wear. For most of the year the differences in power requirements for sustained flight and maneuvering would be considerably less than 4% and 9%, respectively.

As mentioned above, it is possible that a decreased flying surface area may affect birds in other ways, but such possibilities will require more detailed observations. Until then the ecological significance of the reduction in wear remains uncertain for two reasons. First, it is not obvious how fitness scales with energy requirements. Second, the effects of other factors, such as camouflage and countershading, are conceivably at least as important as the savings due to flight energetics and need to be evaluated.

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LITERATURE CITED


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A New Race of Atlapetes leucopterus, with Comments on Widespread Albinism in A. l. dresseri (Taczanowski)

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Recent explorations in the low mountain ridges of northern Dept. Cajamarca, Peru have revealed a startling number of previously undescribed bird forms (Fitzpatrick and O'Neill 1979, Auk 96:443 and references therein). Included in the collections are seven specimens of another distinctive new form in the genus Atlapetes. The form most closely resembles Atlapetes leucopterus dresseri, the southernmost of two previously described races of leucopterus. I here describe the new form as a well-differentiated race of that species but acknowledge the possibility that a narrow geographic hiatus between this form and dresseri may be closed by future collectors, thereby raising the new form to specific status.

In examining specimens of A. l. dresseri, I encountered a striking pattern of individual variation in that race, apparently caused by widespread partial albinism. This is discussed following my description and discussion of the new subspecies.

Atlapetes leucopterus paynteri subsp. nov.

Holotype.—Field Museum of Natural History, no. 299491; adult male from the Cordillera del Condor, above San José de Lourdes, Dept. Cajamarca, Peru, 5º02'S, 78º51'W, elevation approximately 2,200 m; collected 21 July 1976 by J. W. Fitzpatrick.  

Diagnosis.—A small brush finch of the Atlapetes schistaceus species-group (see Paynter 1972, Bull. Mus. Comp. Zool. 143: 297); recognizable as A. leucopterus by small size (wing chord of males 72 mm