

FUNCTIONAL INTERPRETATION OF PROTRUDING FILOPLUMES IN OSCINES¹

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Abstract. The question of the possible function of filoplumes longer than adjacent contour feathers has not previously been addressed for oscines. We studied filoplume location and structure for 117 North American oscine species. Protruding filoplumes (PF) extending beyond the contour feathers occurred regularly in most species but only on the nape and, less frequently, the crown. Species with many PF had relatively flexible and less dense contour feathering on the nape. We hypothesize that PF and other long, nearby, filoplumes are specialized in their relative length to detect disturbance in a part of the feather coat which is not visible to the bird, not accessible for preening with the bill, and which might be especially vulnerable to wind disruption.

Key words: *Filoplumes; North America; oscines; tactile sense.*

INTRODUCTION

Filoplumes, with their long bare rachises and narrow vanes, are believed to serve in tactile monitoring of the positions of contour feathers and perhaps for detecting air currents (Pfeffer 1952; Borodulina 1966; Dmitrieva 1976; Necker 1985a, 1985b). Filoplumes occur widely over the body in most birds (Nitzsch 1867, Pfeffer 1952) but are usually hidden by overlying contour feathers. However, filoplumes protrude beyond the contour feathers in certain species within the Procellariiformes (Imber 1971, James 1986), cormorants (Nitzsch 1867, Pfeffer 1952), and oscines (Newton and Gadow 1893-1896, Witherby 1906). Imber (1971) suggested that the number of protruding filoplumes (hereafter PF) might aid in sexual recognition by certain shearwaters (Procellariidae), but James (1986) opposed this idea, pointing out substantial overlap between the sexes and that nocturnal habits would make PF difficult to see.

For North American oscines, little has been reported about the occurrence of PF, although they have been noted for the American Robin (*Turdus migratorius*; Van Tyne and Berger 1959) and the Scarlet Tanager (*Piranga olivacea*; Stettenheim 1974). Moreover, there has been no explanation for the occurrence of these feathers in the oscines. The goal of our study was to develop a functional hypothesis to explain the presence of PF.

MATERIALS AND METHODS

We examined 2,715 study skins representing 117 North American oscine species in the collections of the New York State Museum, Albany, and the University of Connecticut (UCONN), Storrs. In addition, we studied 18 freshly salvaged specimens representing 13 species and 19 frozen birds representing 12 species. All specimens were examined with a dissecting microscope at magnifications up to 30 power. We analyzed intraspecific variation in PF for wear and for comparison of the sexes using a χ^2 contingency table with $P < 0.05$ taken as the level for statistical significance. Our sampling of filoplumes concealed beneath the contour feathers was less extensive than for PF because nonprotruding filoplumes were more difficult to locate and inspect on study skin specimens; nevertheless, we examined hundreds of nonprotruding filoplumes for a variety of body surfaces and taxa. Selected feathers from frozen specimens were washed with detergent, cleaned by sonication, and examined and photographed by scanning electron microscopy (SEM). In addition, PF on nine live oscines representing eight species were examined with a hand lens.

RESULTS

INTERSPECIFIC DIFFERENCES IN PF

Most species had PF on the nape (Table 1, Fig. 1), and some also had PF on the crown, but PF were not characteristic for any other part of the body. PF on the nape originated from the occiput and were pterylographically contiguous with those on the crown. PF occurred on the crown in 50%

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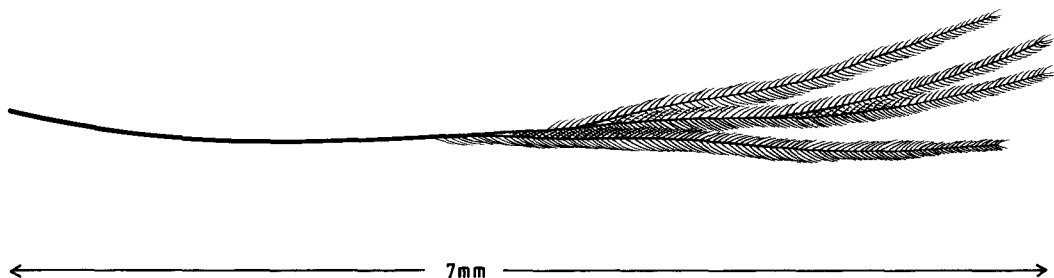


FIGURE 1. Distal end of a filoplume with three worn barbs and lying on the nape of an Ovenbird (*Seiurus aurocapillus*) collected in Connecticut on 26 September 1893 (UCONN 4566).

or more of individuals in *Vireo gilvus*, *Vermivora* (four out of five species), *Dendroica coronata*, *D. virens*, *Mniotilta varia*, *Seiurus noveboracensis*, *S. motacilla*, *Icteria virens*, *Piranga olivacea*, *Pheucticus ludovicianus*, *Passerina cyanea*, *Spizella passerina*, *S. pusilla*, *Molothrus ater*, *Icterus spurius*, *I. galbula*, and *Carduelis pinus*. Unlike their respective congeners, *Seiurus aurocapillus* and *Spizella arborea* lacked PF on the crown.

INTRASPECIFIC VARIATION IN PF

Within a species, birds greatly varied in (1) the number of PF, (2) the length of protrusion of PF beyond the contour feathers, and (3) the number of barbs on PF. Under low magnification, the most worn, filamentous PF appeared to lack barbules, but SEM revealed that remnants of the bases of barbules remained in some cases at least. The wear on PF increased with time since the last molt. For example, in Purple Finches (*Carpodacus purpureus*) only one among 14 study skins from September through February had PF with unevenly broken barbs or missing barbules, while all of 15 from March through August were thus worn ($\chi^2 = 26.3$, $df = 1$, $P < 0.05$).

PF first appeared outside the feather coat on juveniles near fledging. We detected no significant difference between the sexes in occurrence of PF. For example, we compared 25 male American Robins, only three of which lacked PF, with 15 females, all of which had PF ($\chi^2 = 1.9$, $df = 1$, $P > 0.1$).

COMPARISON OF PF WITH OTHER FILOPLUMES

On the head most nonprotruding filoplumes were less than half as long as the adjacent contour feathers. However, species that had PF also had additional long filoplumes that lay concealed beneath the contour feathers near the PF. Moreover, some species lacking PF had relatively long,

nonprojecting filoplumes beneath the contour feathers of the nape, as seen on the Blue Jay (*Cyanocitta cristata*) and Tufted Titmouse (*Parus bicolor*). However, not all oscines lacking PF had such long hidden filoplumes on the nape, as noted for Cedar Waxwings (*Bombocilla cedrorum*). SEM revealed only differences in size, rather than qualitative differences, among PF and nonprotruding filoplumes from the head and other body regions.

RELATION OF PF TO CONTOUR FEATHERS COVERING THE NAPE

Species with many PF had flexible and less dense contour feathering on the nape whereas, in contrast, species with few or no PF often had either relatively stiff contour feathers, e.g., in the European Starling (*Sturnus vulgaris*) or a relatively dense contour feathering, e.g., the two species of shrikes (*Lanius*).

DISCUSSION AND CONCLUSIONS

Why do PF occur in so many oscine species yet not in others? The widespread taxonomic occurrence of PF, particularly on the nape, supports the idea of a special functional role. However, the great individual variation, due at least partly to wear, indicates that many details of these feathers are probably unimportant. In species with PF, the nearby, hidden, long filoplumes very likely serve the same function. Furthermore, in many species typically having PF, some individuals lack PF but presumably always have equivalent long filoplumes hidden beneath the contour feathers and hence should be functionally similar to individuals with PF.

Although numerous functional hypotheses concerning PF are conceivable, we mention here only four that seem most plausible. Inconspicuousness and lack of sexual dimorphism argue

Table 1. Percent of individuals with PF in oscine species, with sample sizes in parentheses.

<i>Eremophila alpestris</i> 0% (53),	<i>Tachycineta bicolor</i> 93% (14),
<i>Stelgidopteryx serripennis</i> 91% (11),	<i>Riparia riparia</i> 88% (26),
<i>Hirundo pyrrhonota</i> 100% (11),	<i>H. rustica</i> 91% (22),
<i>Perisoreus canadensis</i> 0% (9),	<i>Cyanocitta cristata</i> 3% (40),
<i>Corvus brachyrhynchos</i> 0% (17),	<i>Parus atricapillus</i> 42% (12),
<i>P. bicolor</i> 42% (12),	<i>Sitta canadensis</i> 15% (20),
<i>S. carolinensis</i> 18% (17),	<i>Certhia americana</i> 13% (15),
<i>Thryothorus ludovicianus</i> 14% (7),	<i>Troglodytes aedon</i> 69% (13),
<i>T. troglodytes</i> 43% (14),	<i>Cistothorus platensis</i> 0% (7),
<i>C. palustris</i> 0% (12),	<i>Regulus satrapa</i> 48% (21),
<i>R. calendula</i> 88% (16),	<i>Poliophtila caerulea</i> 33% (6),
<i>Sialia sialis</i> 42% (19),	<i>Catharus fuscescens</i> 96% (25),
<i>C. minimus</i> 92% (25),	<i>C. ustulatus</i> 96% (25),
<i>C. guttatus</i> 90% (29),	<i>Hylocichla mustelina</i> 97% (31),
<i>Turdus migratorius</i> 83% (58),	<i>Dumetella carolinensis</i> 77% (26),
<i>Mimus polyglottos</i> 89% (9),	<i>Toxostoma rufum</i> 88% (25),
<i>Anthus spinoletta</i> 88% (8),	<i>Bombicilla cedrorum</i> 0% (42),
<i>Lanius excubitor</i> 0% (12),	<i>L. ludovicianus</i> 10% (10),
<i>Sturnus vulgaris</i> 5% (60),	<i>Vireo griseus</i> 71% (14),
<i>V. solitarius</i> 85% (13),	<i>V. flavifrons</i> 78% (18),
<i>V. gilvus</i> 100% (6),	<i>V. olivaceus</i> 100% (28),
<i>Vermivora pinus</i> 100% (12),	<i>V. chrysoptera</i> 100% (10),
<i>V. peregrina</i> 100% (7),	<i>V. celata</i> 100% (9),
<i>V. ruficapilla</i> 100% (19),	<i>Parula americana</i> 100% (20),
<i>Dendroica petechia</i> 86% (36),	<i>D. pensylvanica</i> 72% (18),
<i>D. magnolia</i> 93% (28),	<i>D. tigrina</i> 92% (12),
<i>D. caerulescens</i> 83% (23),	<i>D. coronata</i> 89% (54),
<i>D. virens</i> 96% (27),	<i>D. fusca</i> 100% (21),
<i>D. pinus</i> 86% (7),	<i>D. discolor</i> 62% (13),
<i>D. palmarum</i> 91% (32),	<i>D. castanea</i> 93% (14),
<i>D. striata</i> 100% (29),	<i>D. cerulea</i> 100% (7),
<i>Mniotilta varia</i> 86% (29),	<i>Setophaga ruticilla</i> 78% (27),
<i>Helminthos vermivorus</i> 100% (6),	<i>Seiurus aurocapillus</i> 93% (27),
<i>S. noveboracensis</i> 100% (18),	<i>S. motacilla</i> 80% (10),
<i>Oporornis formosus</i> 100% (7),	<i>O. agilis</i> 100% (8),
<i>O. philadelphia</i> 100% (12),	<i>Geothlypis trichas</i> 91% (54),
<i>Wilsonia citrina</i> 100% (10),	<i>W. pusilla</i> 89% (9),
<i>W. canadensis</i> 91% (33),	<i>Icteria virens</i> 100% (14),
<i>Piranga olivacea</i> 96% (47),	<i>Cardinalis cardinalis</i> 100% (17),
<i>Pheucticus ludovicianus</i> 96% (25),	<i>Passerina cyanea</i> 100% (18),
<i>Pipilo erythrophthalmus</i> 98% (52),	<i>Spizella arborea</i> 85% (39),
<i>S. passerina</i> 96% (25),	<i>S. pusilla</i> 87% (23),
<i>Poocetes gramineus</i> 21% (28),	<i>Passerculus sandwichensis</i> 60% (57),
<i>Ammodramus savannarum</i> 44% (16),	<i>A. henslowii</i> 0% (8),
<i>A. caudacutus</i> 15% (39),	<i>A. maritimus</i> 72% (18),
<i>Passerella iliaca</i> 100% (21),	<i>Melospiza melodia</i> 91% (66),
<i>M. lincolni</i> 86% (7),	<i>M. georgiana</i> 90% (29),
<i>Zonotrichia albicollis</i> 96% (54),	<i>Z. leucophrys</i> 100% (14),
<i>Junco hyemalis</i> 98% (44),	<i>Calcarius lapponicus</i> 100% (8),
<i>Plectrophenax nivalis</i> 77% (35),	<i>Dolichonyx oryzivorus</i> 93% (27),
<i>Agelaius phoeniceus</i> 93% (69),	<i>Sturnella magna</i> 15% (26),
<i>Euphagus carolinus</i> 54% (26),	<i>Quiscalus quiscula</i> 73% (52),
<i>Molothrus ater</i> 98% (40),	<i>Icterus spurius</i> 100% (13),
<i>I. galbula</i> 100% (26),	<i>Pinicola enucleator</i> 95% (22),
<i>Carpodacus purpureus</i> 90% (29),	<i>C. mexicanus</i> 89% (9),
<i>Loxia curvirostra</i> 82% (28),	<i>L. leucoptera</i> 88% (8),
<i>Carduelis flammea</i> 93% (30),	<i>C. pinus</i> 100% (17),
<i>C. tristis</i> 95% (38),	<i>Coccothraustes vespertinus</i> 88% (17),
<i>Passer domesticus</i> 50% (28).	

against PF serving as display ornaments except perhaps in those species of Old World bulbuls (Pycnonotidae) which have conspicuous PF (Delacour 1943). Although filoplumes might serve to detect air flow during flight (Necker 1985b), no known differences in flight correspond with presence or absence of PF. We also considered that PF might be specialized to detect ectoparasites, but found no association between prevalence of ectoparasites (e.g., see Bennett 1961, Wheeler and Threlfall 1986) and occurrence of PF.

Better evidence on PF function may come from the characteristics of contour feathering covering the nape. Species lacking PF often have either stiff or dense contour feathering on the nape whereas species with well-developed PF have a flexible and less dense contour feathering. Strong winds can readily disrupt the integrity of the feather coat on the nape in the latter group of birds as observed for the Yellow-rumped Warbler (*Dendroica coronata*; unpubl. observ.). Turning to face into the wind restores the smoothness to the feather coat on the nape.

We therefore hypothesize that PF and other relatively long, nearby filoplumes serve to detect disturbances of the feather coat in a region which is not directly visible to a bird, not accessible for preening with the bill, possibly less well insulated than are many other feathered parts of the body, and which may be relatively vulnerable to wind disruption. Under this hypothesis, species lacking PF have either contour feathers that resist loss of insulation by wind or relatively lengthy filoplumes concealed beneath the contour feathers. Furthermore, PF would not be useful on other regions of the body where contour feathering better resists the loss of insulation by wind. Unfortunately, we have been unable to quantify the differences between the kinds of contour feathers. If our hypothesis is correct, there should be significant taxonomic differences in insulation on the nape and crown in wind. Under our hypothesis PF serve in detecting plumage disturbance as do other filoplumes, but the relatively greater length of PF enables better monitoring for surfaces on which disruption of insulation is most likely.

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