———, ———, AND J. S. WAKELEY. 1990. Effects of forest irrigation on long-term trends in breeding-bird communities. Wilson Bull. 102:264–278.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry, 2nd ed. Freeman, San Francisco, California.

SOPPER, W. E. AND L. T. KARDOS. 1973. Vegetation responses to irrigation with treated municipal wastewater. Pp. 271–294 *in* Recycling municipal wastewater and sludge through forest and cropland (W. E. Sopper and L. T. Kardos, eds.). The Pennsylvania State Univ. Press, University Park, Pennsylvania.

STRELKE, W. K. AND J. G. DICKSON. 1980. Effect of forest clear-cut edge on breeding birds in east Texas. J. Wildl. Manage. 44:559–567.

URIE, D. H. 1986. The status of wastewater irrigation of forests, 1985. Pp. 26–40 *in* The forest alternative for treatment and utilization of municipal and industrial wastewater (D. W. Cole, C. L. Henry, and W. L. Nutter, eds.). Univ. Washington Press, Seattle, Washington.

WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of eastern deciduous forests. Pp. 125–205 *in* Forest island dynamics in man-dominated landscapes (R. L. Burgess and D. M. Sharpe, eds.). Springer-Verlag, New York, New York.

YAHNER, R. H. 1986. Structure, seasonal dynamics, and management of avifauna in small even-aged forest stands. Wilson Bull. 98:61–82.

———. 1987. Use of even-aged stands by winter and spring bird communities. Wilson Bull. 99:218–232.

———. 1988. Changes in wildlife communities near edges. Conserv. Biol. 2:333–339.

———. 1991. Avian nesting ecology in small even-aged aspen stands. J. Wildl. Manage. 55:155–159.

———. 1993. Effects of long-term forest clear-cutting on wintering and breeding birds. Wilson Bull. 105:239–255.

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Sequence of plumage evolution in the Standardwing Bird of Paradise.—The faded appearance of the plumage of the Standardwing Bird of Paradise (*Semioptera wallacii*), endemic to Halmahera and Bacan (Batjan) Islands (White and Bruce 1985), is unique within the Paradisaeidae. The dull, unbarred plumage of both sexes is primarily medium brown, darker on the mantle, fading to a pale buffy-white on the remiges (see Gilliard 1969, Cooper and Forshaw 1977). Males possess an iridescent green breast shield and a pair of remarkable elongated wing coverts on each wing. These plumage elaborations have long attracted the attention of ornithologists, while the remainder of the plumage, arguably more interesting in an evolutionary sense, has largely been ignored until Frith (1992).

The phylogenetic relationships of *Semioptera*, a monotypic genus, are poorly known and in dispute. Nearly two-thirds of the fifteen currently recognized genera in the Paradisaeidae (Beehler and Finch 1985, White and Bruce 1985) have been suggested as possible sister taxa of *Semioptera* by taxonomists (see Frith 1992). Given the incredible variety of plumages within this assemblage of genera, especially among males, it is not possible at this time to determine the plumage color and pattern of its ancestor. Nevertheless, several lines of evidence suggest that *Semioptera*'s plumage is aberrant and that the plumage of ancestral populations was predominately black or dark brown.

I examined series of museum skins of *Semioptera* (20+) and all other birds of paradise in the American Museum of Natural History and the National Museum of Natural History (USNM), Smithsonian Institution. Several feathers of one male *Semioptera* (USNM) were sectioned (12 μm) for microscopic examination.

In males of both subspecies, *Semioptera w. wallacii* and *S. w. halmaherae,* the pale grayish-brown crown has plush-like texture. Barbules are macroscopically modified for iridescent refraction but exhibit little structural color at any angle of inspection. Distal barbules (under 430× magnification) consist of a strip of flattened rectangular cells that widen distally without any differentiation into base and pennulum. A few melanin granules or granule vacuoles are scattered within each cell. Barbule flattening is a consistent feature of iridescent feathers (Lucas and Stettenheim 1972).

The intensity of iridescent scaling below the pectoral shield of male *Semioptera* is subdued owing to moderate concentrations of melanin in barbules. In contrast, the strikingly iridescent feathers of predominately black or dark brown birds of paradise (e.g., *Ptiloris* sp., *Parotia* sp., *Lophorina superba, Astrapia nigra*) possess densely pigmented barbule cells (pers. obs.).

With the exception of the adult male's white wing standards, the outer primaries are the palest part of the plumage in both sexes of *Semioptera.* The transition in melanization is gradual from the outermost to innermost remex. The rachises and barb rami of all contour feathers are pale-buffy white to white. Contrast between the distal and proximal ends of contour feathers is less than in possible sister taxa. Likewise, the contrast between dorsal and ventral plumage, countershading (Thayer 1896), is minimal in both sexes of *Semioptera.* Additionally, concentrations of melanin are low in the keratinized soft parts (Cooper and Forshaw 1977). By comparison, the rachises and webs of primaries are heavily pigmented with melanins in other birds of paradise, particularly at the tips, probably as an adaptation to reduce abrasion and wear (Burtt 1981). In sum, the absence of heavy melanization of the plumage and softparts in both sexes of *Semioptera* suggests a common genetic cause and a derived condition.

The aberrant plumage of *Semioptera* may be due to one of two possible genetic mutations. One possibility is a fixed non-eumelanic schizochroism (Buckley 1982), producing a "fawn variant." In other words, the pigment that produces black coloration (eumelanin) is absent, leaving only residual phaeomelanins, which impart a warm brown color to *Semioptera*'s plumage. The second possibility is that the density of one or several pigments has been uniformly diluted. Examples of "faded" plumage, possibly due to schizochroism or dilution, have been reported in the bird of paradise species *Cnemophilus loriae* (Frith 1987) and *C. macgregorii* (Frith and Harrison 1989). Whatever the underlying cause of *Semioptera*'s faded appearance, it appears to be genetically fixed.

Although the genetics of plumage coloration in wild birds is poorly understood, inheritance of schizochroism is recessive in several well-studied cagebirds (Buckley 1982). The morphology and color of avian plumage may be encoded by dozens or hundreds of genes. However, schizochroic mutations might involve a single regulatory gene, for instance, an inhibitor of the enzyme tyrosinase, which is necessary for melanin synthesis. In any event, it would seem that many more genes are involved in encoding the complex ultrastructure of *Semioptera*'s crown feathers than in their pigmentation. The peculiar condition of pigmentation in *Semioptera* appears to be unique as a species-specific characteristic within the Paradisaeidae.

Island isolation and the absence of other polygynous birds of paradise may have permitted a relaxation of plumage stereotypy in the ancestral population of *Semioptera.* In a lek breeding system, a pale-winged mutation might have been rapidly fixed by sexual selection. The development of leucistic wing standards may also be linked to the mutation. Corresponding plumage patterns in females are probably caused by correlated selective responses between the sexes (Lande 1980). Frith (1992) concluded that the whitish primaries of *Semioptera* were as important a component in the aerial display of lekking male *Semioptera* as the breast shield and wing standards. Wing tips are also fluttered, vibrated, and spread during the wing standard display. In fact, sexual selection for contrasting visibility of the primaries and wing standards in males may be driving progressive leucism in *Semioptera*. If true, the iridescence of the heavily melanized crown feathers in ancestral populations may have been degraded by the emergence of a more sexually favored leucistic trait in descendent populations. Because the two subspecies differ only slightly in the degree of crown iridescence, the mutation resulting in their faded appearance undoubtedly occurred in the founder population before separation and differentiation on Halmahera and its land-bridge island, Bacan.

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LITERATURE CITED

BEEHLER, B. M. AND B. W. FINCH. 1985. Species-checklist of the birds of New Guinea. Aust. Ornithol. Monogr. 1:1–126.

BUCKLEY, P. A. 1982. Avian genetics. Pp. 21–110 *in* Diseases of cage and aviary birds, 2nd ed. (M. Petrak, ed.). Lea and Febiger, Philadelphia.

BURTT, E. H., JR. 1981. The adaptiveness of animal colors. BioScience 31:723–729.

COOPER, W. T. AND J. M. FORSHAW. 1977. The birds of paradise and bowerbirds. Collins, Sydney, Australia.

FRITH, C. B. 1987. An undescribed plumage of Loria's Bird of Paradise *Loria loriae*. Bull. Brit. Ornithol. Club 107:177–180.

———. 1992. Standardwing Bird of Paradise *Semioptera wallacii* displays, with comparative observations on those of other Paradisaeidae. Emu 92:79–86.

——— AND C. J. O. HARRISON. 1989. An undescribed plumage of the Crested Bird of Paradise *Cnemophilus macgregorii*. Bull. Brit. Ornithol. Club 109:137–140.

GILLIARD, E. T. 1969. Birds of paradise and bowerbirds. Weidenfeld & Nicholson, London, England.

LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305.

LUCAS, A. M. AND P. R. STETTENHEIM. 1972. Avian anatomy—integument. Agric. Hdbk. 362. U.S. Dept. Agric., Washington, D.C.

THAYER, A. H. 1896. The law that underlies protective coloration. Auk 13:124–129.

WHITE, C. M. N. AND M. D. BRUCE. 1985. Birds of Wallacea (Sulawesi, Moluccas and Lesser Sunda Islands). BOU checklist series, London, England.

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