

STUDY OF PLUMAGE OF THE FOUR SPECIES OF THE GENUS *GALLUS*

G. VICTOR MOREJOHN

Department of Biological Science
San Jose State College
San Jose, California 95114

Among the many species of birds known, perhaps the one most important to man throughout the ages has been the domestic fowl. The original domestication of this bird antedates history. Yet even today, we cannot conclusively state whether or not it has had monophyletic origin from one of the wild species or polyphyletic origin from two or more of the living four species. There is evidence to support both theories.

In an attempt to elucidate further the question of monophyly or polyphyly, an investigation was begun with the four species of the genus *Gallus*. It was believed that a close study of internal anatomy, plumage, behavior, and reproduction would yield information helpful in interpreting the evolution of the domestic form. A recent study (Morejohn 1966) revealed significant differences in the syringial apparatus of three species. The present investigation is a close study of feather types and plumage sequences of the four species. The conclusions drawn as a result of this study are relevant to the interrelationships of the four species. Conclusions relative to the relationships of the junglefowls to the domestic fowl will be reported in another paper.

The issues that exist currently with respect to nomenclature of avian plumages and molts

TABLE 1. Classification of cock plumage: unspecialized primitive (0), slightly specialized (X), and highly specialized (XX). See text for explanation.

Feather tract	<i>gallus</i>	<i>varius</i>	<i>sonneratii</i>	<i>lafayettei</i>
Upper neck	X	0	XX	X
Midneck	X	X	XX	X
Lower neck	X	X	XX	X
Upper back	X	0	0	X
Lower back	X	X	X	X
Rump	X	X	XX	X
Upper tail coverts	X	X	X	X
Lower tail coverts	0	0	0	0
Lesser wing coverts	X	X	XX	X
Median wing coverts	0	X	XX	X
Greater wing coverts	0	0	0	0
Upper breast	0	0	0	X
Midbreast	0	0	0	X
Lower breast	0	0	X	X

will not be considered here, and the reader is referred to the most recent review presented by Amadon (1966).

MATERIALS AND METHODS

Feathers from 14 different tracts (tables 1 and 2) were compared as to shape, specializations, and pigmentation in adult males and females and immature birds. Particular emphasis was placed on the study of the feathers of interspecific hybrids. The eclipse plumage was studied in live *G. sonneratii* and in the interspecific hybrid *G. sonneratii* × *G. gallus*.

The following is a list of study skins examined:

Species	♂ ♂	♀ ♀
<i>Gallus gallus</i>	10	12
<i>Gallus lafayettei</i>	3	3
<i>Gallus sonneratii</i>	8	10
<i>Gallus varius</i>	3	3
Interspecific hybrids		
<i>G. gallus</i> × <i>G. varius</i>	2	2
<i>G. gallus</i> × <i>G. sonneratii</i>	10	15

The use of the word "specialized" in this paper refers to the degree of change in form or color from the plumage or feathers found in the female. The feathers of the females of this genus are taken as a standard of primitiveness; the feathers are dull, protectively colored, and simple in form. The general areas under consideration may be grouped as follows: neck, back, rump, tail, wings, and

TABLE 2. Classification of hen plumage: stippling (S), barring (B), pencilling (P), and solid color (C).

Feather tract	<i>gallus</i>	<i>varius</i>	<i>sonneratii</i>	<i>lafayettei</i>
Upper neck	S	P	P	P
Lower neck	S	P	P	S
Back	S	P	S	S
Rump	S	P	S	S
Upper tail coverts	S	B	S	S
Lower tail coverts	S	B	S	S
Lesser wing coverts	S	B	S	S
Median wing coverts	S	B	S	S
Greater wing coverts	S	B	S	B
Upper breast	C	P	P	P
Lower breast	C	S	P	P
Secondaries	S	B	P	B
Tail	S	B	S	S

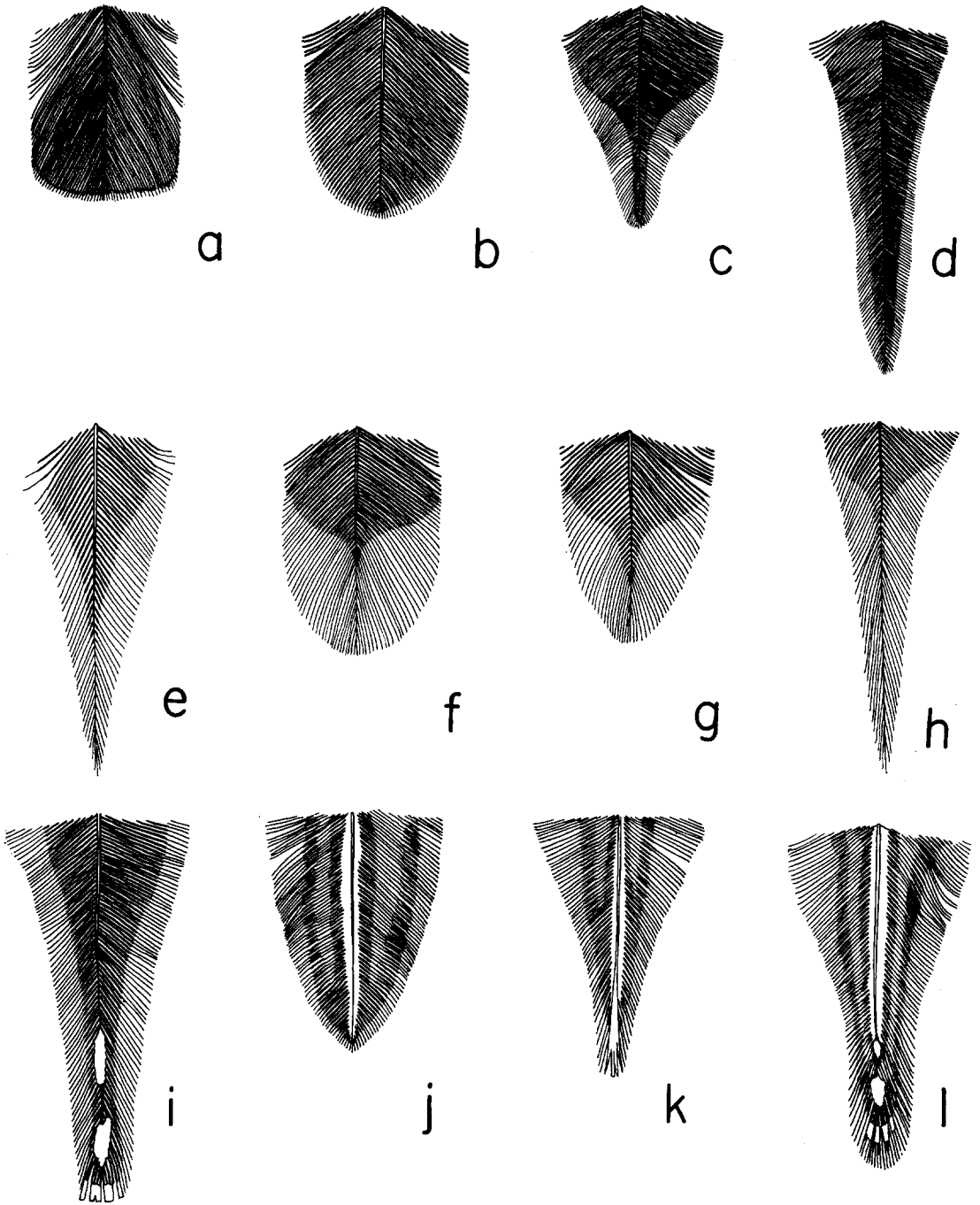


FIGURE 1. Representative feathers from cocks of the three species of junglefowl: (a) *G. varius*, truncate neck hackles; (b) same, henlike feather of the back; (c) same, lesser wing covert; (d) same, rump saddle hackle; (e) *G. gallus*, lanceolate neck hackle showing fringed area lacking barbules; (f) same, back; (g) same, lesser wing covert; (h) same, rump saddle hackle; (i) *G. sonneratii*, neck hackle showing expanded waxlike rachis and shredded tip; (j) same, back; (k) same, lesser wing covert; (l) same, saddle hackle.

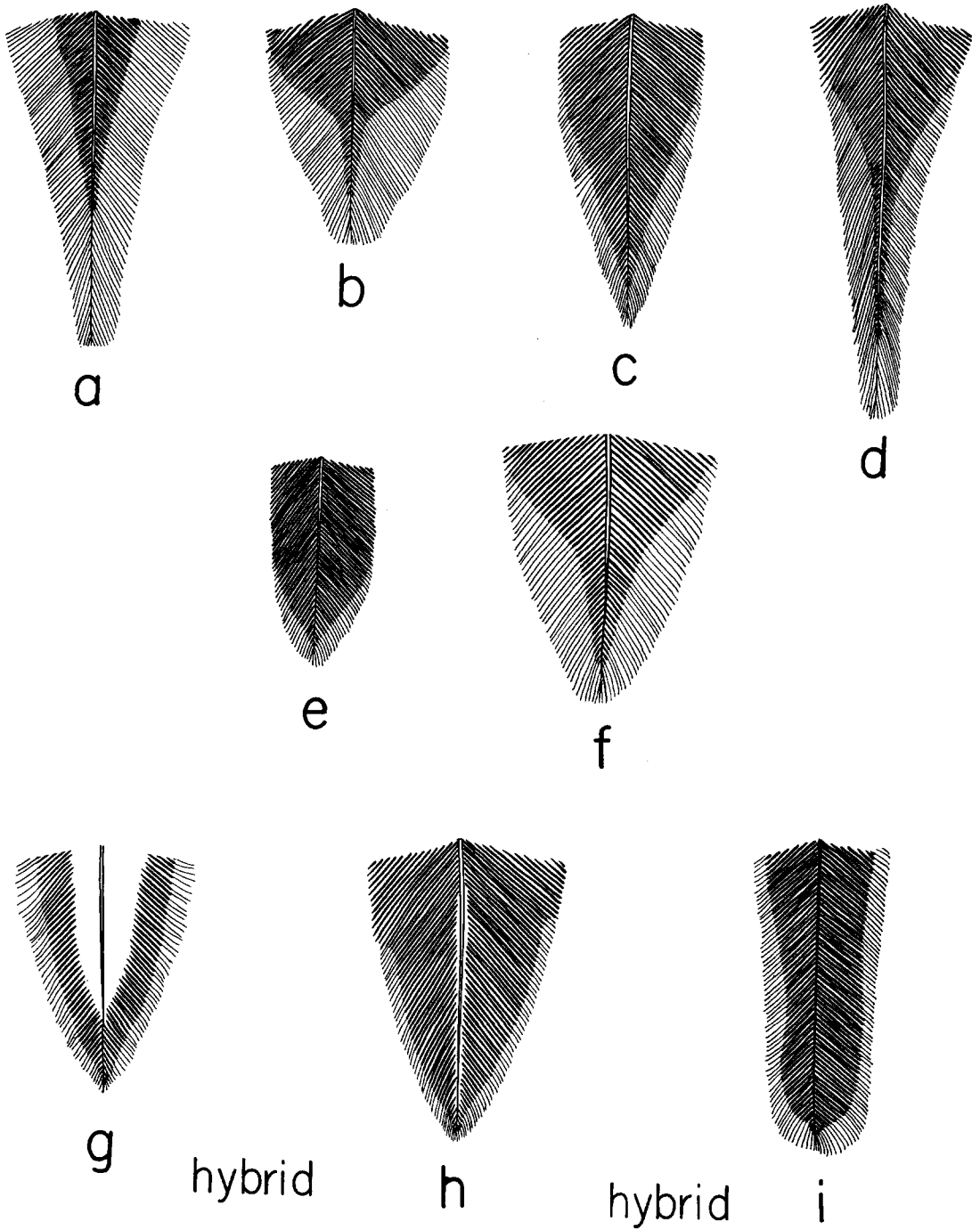


FIGURE 2. Representative feathers from *G. lafayetii* and F_1 interspecific hybrids: (a) *G. lafayetii*, neck hackle; (b) same, back; (c) same, median wing covert; (d) same, rump saddle hackle; (e) same, upper breast; (f) same, lower breast showing strong dimorphism; (g) F_1 hybrid (*gallus-sonneratii*), breast; (h) same, back; and (i) F_1 hybrid (*gallus-varius*), elongate neck hackle with truncate tip.

breast. Gradients of increasing feather specialization are found in each feather tract of males. Within each tract the gradient usually is directed posteriorly and ventrally. The feathers of all species of this genus exhibit differences in structure (dimorphism) and color (dichromatism). Although feathers that show dimorphism also show dichromatism, not all dichromatic feathers on males differ morphologically from comparable feather tracts on females.

SPECIES COMPARISONS

MALES

Other than plumage, voice, and other behavioral traits, the major morphological differences among the species are found in the median upright comb and the gular wattles. In *G. varius* the comb is unserrated, and there is only one median wattle. In the other three species the comb is serrated, and there are two wattles. The greater number of tail feathers (16) in both sexes of *G. varius* and the truncate shape of the neck hackles of *G. varius* males (fig. 1a) differentiate this species from the others on the basis of plumage morphology. The other three species typically possess 14 tail feathers and lanceolate, fringed neck hackles.

The only specialized feathers (morphologically) in *G. varius* males are found on the neck, rump, tail, and wings. The feathers of the back (fig. 1b), breast, and greater wing coverts do not differ markedly in shape from the female type. The neck, back, and rump feathers of male *G. gallus* (fig. 1e, f, h) and *G. lafayetii* (fig. 2a, b, d) are very similar in form and color; they are fringed and lack barbules in the outer edges. The lesser wing coverts differ primarily in color and only slightly in shape. The median wing coverts in *gallus* are female-shaped, and in *lafayetii* they are specialized (fig. 2c). The greater wing coverts of both *gallus* and *lafayetii* are similar in shape but not in color. The striking difference between *gallus* and *lafayetii* is the shape of the breast feathers. The feathers of *gallus* are femalelike (rounded), whereas *lafayetii* has highly modified breast feathers that are pointed and fringed (fig. 2f). A peculiarity of *lafayetii* is the large spot of bluish-purple feathers that appears on the upper breast near the lower neck region (fig. 2e). The rump region also has feathers of this type dorsally but laterally has a typical *gallus*-like lanceolate feather. Certain feathers of *sonneratii* differ from those of the other species in possessing sealing-waxlike spots. These spots are actually expanded and flat-

tened portions of the rachis. Toward the apex of the feather the flattened rachis becomes shredded (fig. 1i), and the feather takes on its extraordinary appearance. The spots resemble those found on the feathers of waxwings, *Bombycilla* (Kimball 1959). Morphologically (with the exception of the waxy areas) *sonneratii* and *lafayetii* resemble each other in having the lesser and median wing coverts and breast feathers specialized, in contrast to the similarity in *varius* and *gallus*. Highly fringed feathers were found to be more numerous in *lafayetii*, especially on the breast. (See table 1 for male plumage comparisons.)

A distinctive characteristic of *gallus* males not shared by other species is the large fluff of down (after shafts) at the base of the tail sickles. This characteristic is usually prominently displayed when calling hens or during challenging attitudes, and it can otherwise be seen easily in contrast to the total lack of it in *sonneratii*, *lafayetii*, and *varius*.

FEMALES

The shape of feathers in hens is virtually the same in the four species. The main differences are found in the distribution of pigment. Table 2 summarizes the characteristics of stippling, pencilling, and barring in the plumage of the hens. The feathers of the back and rump of *varius* females are pencilled (fig. 3a). This pattern closely resembles the pencilling found in domestic dark Cornish hens. The rest of the plumage of *varius* hens is irregularly barred (fig. 3b) with the exception of the breast. The upper breast consists of light brown-colored feathers with a dark-brown edge (fig. 3c). The lower breast feathers are light brown or salmon-colored. In *lafayetii* hens only the greater wing coverts and the secondaries show a barred pattern similar to that in *varius* hens. The remainder of the plumage with the exception of the breast is stippled light brown (fig. 3d). Many of the breast feathers of *lafayetii* females have a light-buff to whitish background with imperfect pencilling (fig. 3e). Both *gallus* and *sonneratii* females have uniformly stippled light-brown plumage on the back, rump, tail, and wing coverts (fig. 3d). The breast feathers of *gallus* hens, however, are light salmon-colored (fig. 3f), whereas the breast feathers of *sonneratii* hens are white with black edges (fig. 3g). The rachis of most stippled feathers in these two hens is usually light straw-color. The vane areas immediately adjacent to the light-colored rachis in some *sonneratii* and *gallus* hens, however, may also

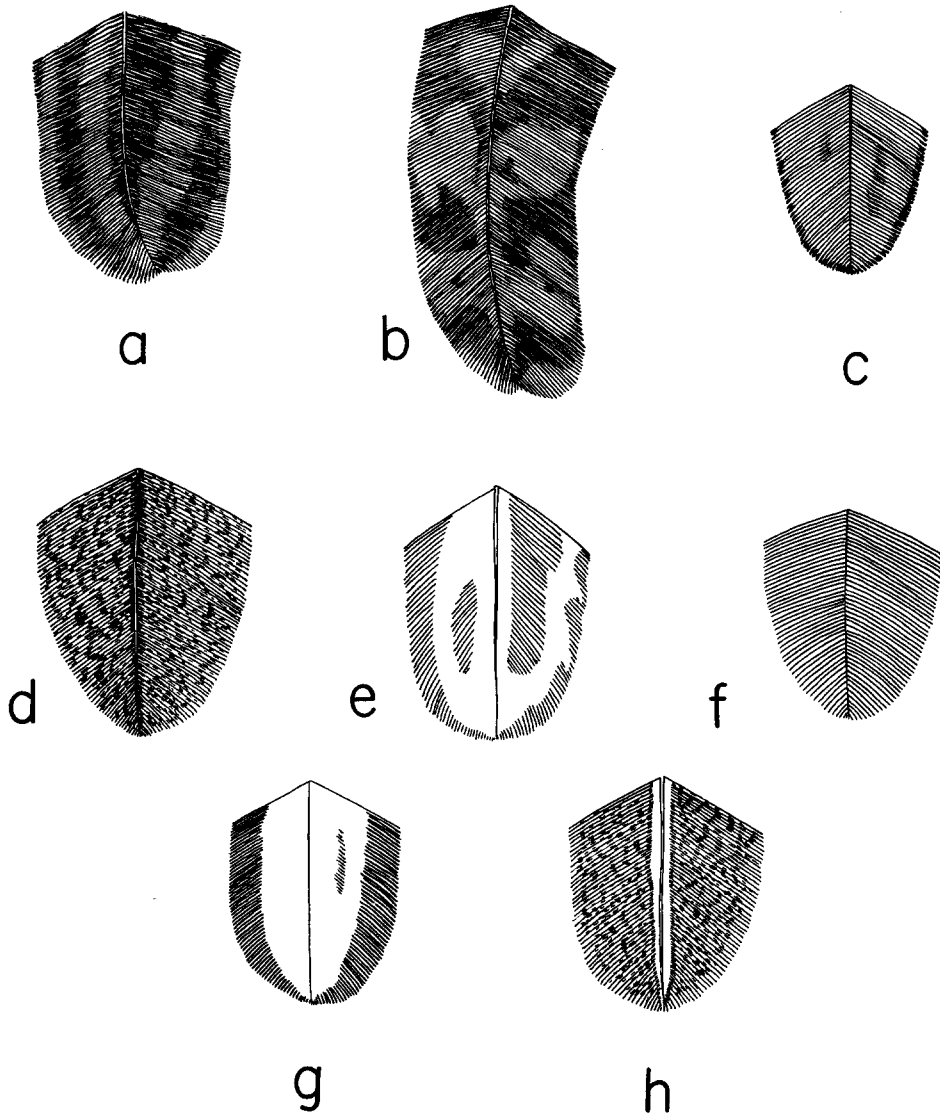


FIGURE 3. Representative contour feathers from hens of the four species of junglefowl: (a) *G. varius*, back showing pencilling; (b) same, median wing covert, showing barring; (c) same, upper breast; (d) stippled feather typical of the back, rump, tail, and wing coverts of *gallus* and *sonneratii*; (e) *G. lafayetii*, midbreast, showing imperfect pencilling; (f) salmon-colored breast feather found on *G. gallus* and *G. varius*; (g) *G. sonneratii*, midbreast; (h) same, stippled feather showing light-colored areas adjacent to the rachis.

be light-colored, giving the bird a distinctly streaked appearance dorsally (fig. 3h). The outer vanes of secondaries and tail feathers are stippled in *gallus* and *sonneratii* females, but the same feathers are barred in *varius* and *lafayetii* females.

PLUMAGE SEQUENCE

NORMAL SEQUENCE

The juvenal and immature plumage for known-age birds was studied in a limited series of individuals of *gallus*, *sonneratii*, and F_1 hybrid (*G. gallus*-*G. sonneratii*). The

sequence of plumage types in the two species was: natal down, juvenal, immature, adult. After the down plumage, three distinct plumage types are grown and molted, inclusive of the contour feathers of the body, wing, and tail. The feathers of the juvenal plumage of hens differ from the other two plumage types only slightly; the feather patterns and coloration are not as perfectly developed as in the immature and adult. Indeed it is a task to be able to distinguish the immature from the adult female plumage without close inspection of the bird to see the developing feather shafts of the emerging plumage.

The juvenal plumage of male *gallus* and *sonneratii* grossly resembles the corresponding female juvenal plumage, but upon closer examination it is different. The male birds are protectively colored in their respective browns and greys; the neck hackles are darker, and in the case of *sonneratii* these neck feathers resemble the "eclipse" plumage (described below) of adult males. The immature plumage of *gallus* and *sonneratii* males differs only in degree of specialization from the adult plumage, and the feathers are not as long and glossy as in the adult. In the case of *sonneratii* males, however, the secondaries of the wings of adult first-year birds have stippled outer vanes. Birds older than two years have entirely black secondaries with light-colored rachises. (I do not believe that a minor difference such as differently colored secondaries necessitates calling the second-year plumage by a different name other than adult.) On the other hand, adult *gallus* males have stippled brown outer vanes on secondaries in all plumages of all ages.

ECLIPSE PLUMAGE

An interesting aspect of this plumage study was the molting sequence of adult plumage better known as the "eclipse." This plumage is well represented in the species of ducks that as adults have feathers that differ dimorphically and dichromatically. In other species in which the sexes do not differ materially in plumage, the eclipse is not apparent. Van Tyne and Berger (1959) state that a similar type of plumage change is also found in the bee-eaters (Meropidae), cuckoo-shrikes (Campephagidae), sunbirds (Nectariniidae), and weaver finches (Ploceidae). Typically, drakes molt the adult plumage toward the end of the breeding season and assume somber-colored plumage similar to that of the adult females. This femalelike (eclipse) plumage of drakes is shed four to 10 weeks later, at which time the growth of adult plumage replaces it. Baker (1930), Delacour (1951), and Kimball (1959) mention the occurrence of this plumage in males of the three species of junglefowl, *gallus*, *lafayetii*, and *sonneratii*. This plumage is reported to occur in summer during or after the breeding season. Detailed studies on the eclipse plumage in ducks have been carried out, but no work heretofore has been done with the junglefowls. The fact that the eclipse is not necessarily restricted to species of ducks having brightly colored males or, for that matter, to males alone was conclusively demonstrated by Stead (1938a,

1938b). He found that the Grey Duck (*Anas superciliosa*), in which the sexes are similar in color and shape of plumage, molted their breeding plumage (in this case the same type of plumage as the nonbreeding plumage or adult) and acquired a new plumage that was again molted in a few weeks. Flight and tail feathers were replaced only once, however. This type of molt was also observed in the Canada Goose and both White and Black Swans. This peculiar double molt was found to take place within a matter of several weeks in junglefowl also; however, it was restricted only to the cervical feather tract (neck hackles).

Goodale (1916) was one of the first to conduct experiments that shed some light on hormonal control of the eclipse plumage in ducks. He found that complete removal of gonads of either sex, regardless of age and plumage, resulted in the development of a breeding plumage of the adult male that, after successive molts, showed no change in phenotype. Walton (1939) repeated similar gonadectomy experiments on wild mallards and employed increased day-lengths during the normal short-day periods of the year. He found that adult drakes castrated in fall or spring, before or after eclipse, reacted alike; castration did not prevent assumption of eclipse plumage during the first year. In the following years, however, eclipse plumage was not again acquired. Swetosarow and Streich (1937) found that drakes castrated between September and April did not eclipse, whereas those castrated between May and August did.

Walton (1939), was able to produce a full eclipse plumage prematurely in February. He offered no explanations for his results, but it is obvious from his work that the length of the photoperiod plays an important part in the initiation of the eclipse plumage in mallards.

HORMONAL REGULATION OF PLUMAGE SEQUENCE

EXPERIMENTAL PROCEDURE

A close study of feather changes during the adult molt in *Gallus sonneratii* and the interspecific hybrid (*G. sonneratii* × *G. gallus*) was made in the present investigation and demonstrated that only the neck hackles acquired an eclipse-type feather. These feathers were much shorter, dark gray or brown stippled, with no male specializations (fig. 4). For unknown reasons the specimens of *G. gallus* available for study did not have an

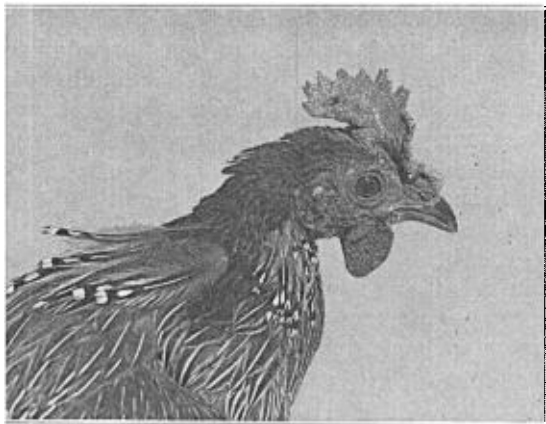


FIGURE 4. Adult male *Gallus sonneratii* in process of molting neck hackles and assuming eclipse plumage.

eclipse plumage; however, the species is known to undergo eclipse similar to *sonneratii* (Morejohn, field observations in India and Burma; Kimball 1958). A series of experiments was devised to determine gonadal hormone effects on the eclipse. Males and females were used, and since the F_1 hybrid (*gallus-sonneratii*) males did undergo eclipse some were employed. No gonadectomy experiments were conducted with *sonneratii* males since only two males were available and necessary as breeding birds. The method employed has been used by the author in similar experiments with gallinaceous birds (Morejohn 1953, 1955, 1961). Six hybrids were castrated, three of which were also given 15 mg of diethylstilbestrol pellets in the skin of the neck. Three other intact hybrid males were given diethylstilbestrol pellets, and three hybrid males were used as controls. Of the two *sonneratii* males available, one was given diethylstilbestrol and the other used as a control. The experimental birds were gonadectomized in January, and implants of diethylstilbestrol were made in March—more than a month prior to noticeable loss of neck hackle feathers.

RESULTS

The only noticeable effect of the experiments was the feminization of subsequently grown feathers in all implanted birds. Castration and diethylstilbestrol had no effect whatsoever in altering the timing of the eclipse. Feather samples taken from all feather tracts before, during, and after eclipse in experimental males as well as normal females demonstrated that hens as well underwent a double molt. Although hens have only one feather type, it was observed that they also

shed feathers of the neck and regrew them within several weeks. In other words, hens lost normal female neck hackles, replaced them with the same type feather and then shed these feathers within a six-week period and replaced them with the same feather type. The eclipse as such, therefore, affects both sexes and is only clearly discernible in males owing to the different color and shape of the eclipse hackles. The castrated F_1 cocks were kept over another year and assumed normal eclipse hackles during the summer. Thus castration in these birds did not prevent subsequent assumption of eclipse as it does in ducks.

Observations on the eclipse in *sonneratii* cocks and F_1 hybrids showed that a decided decrease in vigor, fertility, and aggressiveness and a lack of crowing were manifest in these birds at this time. Interestingly, however, if several Red Junglefowl hens, actively laying eggs, were kept with cocks about to eclipse (this was done to determine cock fertility), the onset of the eclipse was delayed for perhaps a month, and the behavioral characteristics of cocks in eclipse were not as noticeable. The *sonneratii* males during eclipse lost the bright crimson-red color of their legs, and their combs and wattles decreased, perhaps, to half their total size. The interspecific hybrids *gallus-sonneratii* were not affected to the same degree, although the red color of their legs, which is restricted to the lateral and posterior edges and some of the frontal scutes of their legs, did fade considerably. *G. varius* has been reported (Delacour 1951) not to undergo eclipse.

INTERSPECIFIC HYBRIDS

Interspecific hybrids between *gallus* and *sonneratii*, and *gallus* and *varius* were also studied. Generally speaking, intermediacy of plumage types was the rule. In contrast to the work of others (Beebe 1918–22; Lotsy and Kuiper 1924), the hackles of the neck of F_1 *G. gallus-G. sonneratii* cocks did not show dominance of peculiar waxlike expansions of the rachis of *sonneratii*. There were definite areas of color that suggested the character, but it was clearly absent in the neck hackles, lower wing and median wing coverts. The feathers of the back (fig. 2h), however, closely resembled those of *sonneratii*, and had little of the fringed dimorphism typical of *gallus*. The feathers of the breast were decidedly pointed (fig. 2g), similar to those of *sonneratii*, and many of them resembled the latter in color; some feathers, however, were nearly all white with a slight gold tinge

to the apex. Other feathers of the lower breast were fringed and resembled the corresponding feathers of *lafayetii*, but not of either parent (*gallus* or *sonneratii*). The lesser and median wing coverts of *sonneratii*, in contrast to *gallus* (table 1), were both highly specialized, exhibited strong dimorphism, and possessed greatly flattened rachi of waxlike material at the feather tips. The median wing coverts of the hybrid (*gallus-sonneratii*), however, showed weak dimorphism; these feathers closely resembled again in shape the same feathers of the nonparent *lafayetii* (fig. 2c). The prominent white basal tail fluff of *gallus* was incompletely dominant in these hybrid males, and it was not as prominently displayed.

The hybrid hen (*gallus-sonneratii*) strikingly resembled the *lafayetii* hens.

The F₁ hybrid *gallus-varius* cocks showed the influence of *gallus* genes by the presence of red pigment in the region of the back and rump, lengthened neck hackles (fig. 2i), and fringed dimorphic feathers on the back. In contrast to the *gallus-sonneratii* hybrid males the tail fluff was absent in the male hybrids of *gallus* and *varius*. Double gular wattles and serrated comb were inherited from *gallus*.

The hybrid *gallus-varius* hen, in adult plumage, had feathers on the back, rump, upper tail coverts, lesser median and greater wing coverts that differed from the same feathers of hens of both parental species. The feathers of the hybrid hen were pencilled in the feather tracts mentioned. In *gallus* hens the same feather tracts were stippled; in *varius* hens they were mostly barred (see table 2 for *gallus* and *varius* hens). The outer vanes of the secondaries were barred as in the *varius* parent. The breast feathers, however, were typically salmon-colored as in the *gallus* parent, although the *varius* hen also showed some salmon color in her breast.

DISCUSSION

It is generally conceded that primitive characteristics are generalized in nature (Mayr 1942: 294). The recent monographic studies of De Beer (1954) on *Archeopteryx* confirm the avian affinities of this animal despite Lowe's (1944) contention that the skeleton is more reptilian than avian. De Beer found the feather structure of *Archeopteryx* to be typical of that of recent flying birds. The flight feathers, wing coverts, and rectrices of this fossil have rounded outlines indicating, at least, lack of morphological specialization.

The evolution of dichromatism and dimorphism have had a complex and possibly in-

dependent development intricately associated with sexual selection on the part of the female (Sibley 1957). The lack of morphological specialization of the neck and back feathers in *varius* may truly reflect an ancestral condition. The eclipse plumage common only to the other three species may, in fact, be a reflection of the ancestral nature of this tract, since in shape and color (without metallic iridescence) the eclipse hackles of males of the other three species resemble the neck hackles of *varius*.

The close relationship of the four species to each other is further borne out when they are compared as to plumage color and shape of plumage alone. Lotsy and Kuiper (1924) found that many characteristics are shared by all. Limiting the comparison to color, however, several gross comparisons may be made. The males of *gallus* and *varius* are similar on the ventral surface, which is black. Dorsally *gallus* and *lafayetii* are very similar, both having varying shades of reds and yellows. In hens the ventral surface of *lafayetii* and *sonneratii* are very similar, while dorsally the feather patterns of *gallus* and *sonneratii* strongly resemble each other. Wing bars are also shared by *varius* and *lafayetii* females. The feather specialization of the males of the four species makes it apparent that *varius* and *sonneratii* are at the ends of two extremes. Furthermore, *varius* does not share any of the color characteristics with *sonneratii*; hence, when all traits are considered, they are probably the most distantly related.

It is possible that in the evolution of the genus two species became differentiated—an insular form, *varius*-like, and a mainland form ancestral to *gallus*, *sonneratii*, and *lafayetii*. The mainland form may have eventually differentiated into two distinct species, *gallus*-like, east and north of the Godaverri river, and *sonneratii*-like, west and south of the Godaverri. The present mouth of the Godaverri is only a few hundred miles north of Ceylon. The island was once part of the Indian peninsula, and today it is still connected to the mainland by a man-made bridge. The species *lafayetii* may represent a specialized relict of the ancestral mainland form. The F₁ hybrid (*gallus-sonneratii*) hens resemble *lafayetii* hens to a marked degree. Morphologically, the feathers of the corresponding F₁ cock significantly resemble the feathers of the male *lafayetii*. The red-breasted mutant recently described by Kimball (1954) alters the phenotype of a *gallus* cock to such a degree (normal black breasts become red) that grossly the resemblance to *lafayetii* cannot be mistaken.

What effects the red-breasted gene would have in an F₁ hybrid (*gallus-sonneratii*) can only be surmised. The specialized rachis of *sonneratii* apparently is recessive since it does not appear in any first-generation hybrids between the other species or domestic fowl. It can be recovered, however, in nearly perfect state in some individual males of black-cross progenies (Danforth 1958) when F₁ individuals are crossed back to the *sonneratii* parent. The feathers on the back of *sonneratii* males are modified only to a slight degree, whereas those of *gallus* in the same region are highly modified. The F₁ *gallus-sonneratii* male likewise resembles *lafayetii* in this respect, again demonstrating how gene recombinations may express parental similarity on the assumption of *lafayetii*-like ancestral mainland form.

It is well known that the females of most phasianid species of the same genus are extremely similar in color and that the corresponding males are strikingly distinct (Delacour 1951; Sibley 1957). Sexual selection by females based mainly on vision has resulted in selection of genes governing feather traits in cocks that can only exert their action in the absence of estrogen. The inhibitory effect of estrogen on male plumage of different genotypes has been demonstrated by Morejohn (1953, 1955), and the assumption of cock plumage by ovariectomized hens has been amply studied by Domm (1927, 1929). Amadon (1966), however, states the reverse to be the case for *Gallus gallus* but does not refer to experimental evidence in support of his statement.

A classification of patterns of definitive plumages in birds has been suggested by Humphrey and Parkes (1959). The three main patterns described are: (1) one complete molt and one plumage per cycle; (2) two molts and two plumages per cycle: (a) prealternate molt partial and (b) prealternate molt complete; and (3) three molts and three plumages per cycle: (a) presupplemental molt follows basic plumage and (b) presupplemental molt follows alternate plumage.

On the basis of the studies reported herein, the three species of jungle fowl that undergo eclipse are classifiable under heading (2) above of Humphrey and Parkes, *i.e.*, two molts and two plumages per cycle with one a partial prealternate molt. It is assumed that ancestrally both sexes of junglefowl were alike in color and that the breeding or adult plumage of the male was acquired as an alternate plumage maintained under physiological control, perhaps for a shorter period of time than now

exhibited. It is conceivable that the duration in time that the plumage was worn increased, and that all feather tracts, with the exception of the neck hackles, eventually assumed a permanent adult plumage dichromatically and dimorphically different than the female. The neck hackles, thus, would be the only feather tract retaining the double molt trait, and in the cock assumes a femalelike feather shape (unspecialized) during the eclipse molt.

SUMMARY

The plumages of the four species of junglefowl were compared. In general, it was found that the plumage of *varius* cocks was distinct in form. The cocks of the other three species resembled each other in form and color, but *sonneratii* cocks have the most specialized plumage. The hens of the four species resembled each other closely, some with certain characteristics not possessed by others.

The sequence of plumages was studied in two species. After the down plumage, both species acquire a juvenal plumage, then an immature plumage, and finally a definitive adult plumage. Body feathers as well as flight and tail feathers are replaced at the same time.

A study of the cocks and hens of the interspecific hybrids *gallus-sonneratii* and *gallus-varius* brought out some interesting aspects of the inheritance of plumage characteristics. The peculiar waxlike expansions of the rachis of *sonneratii* cocks were found to be recessive in crosses with *gallus*. The truncate shape of neck hackles of *varius* males was incompletely dominant to the pointed lacy feathers of *gallus* males. The pointed breast feathers of *sonneratii* cocks were dominant to the rounded feathers of *gallus*. Some feathers produced by the *gallus-sonneratii* hybrid cock resembled the feathers of the same tract on *G. lafayetii*. The basal tail fluff of *gallus* was incompletely dominant in the *gallus-sonneratii* hybrid, but recessive in the *gallus-varius* hybrid. Feathers on the breast and back of *gallus-sonneratii* hens markedly resembled the feathers of the *lafayetii* hen. Hybrid *gallus-varius* hens become pencilled in feather tracts that were not pencilled in parents.

The eclipse plumage of *sonneratii* and interspecific hybrid *gallus-sonneratii* cocks was also investigated. Only the feathers of the neck are affected. The ability to undergo eclipse has dominant inheritance. Castration of hybrids had no immediate or prolonged effect on the assumption of the eclipse feather

in the neck region. Estrogen implantations did not prevent molting of neck hackles. Hybrid and *sonneratii* hens also underwent a double molt of the neck feathers at the same time that the cocks were undergoing eclipse.

ACKNOWLEDGMENTS

Many thanks are extended to the American

Museum of Natural History, the United States National Museum, the Los Angeles County Museum of Natural History, and University of California Museum of Vertebrate Zoology for extended use of study skins. K. E. Stager of the Los Angeles County Museum of Natural History kindly donated a frozen specimen of *Gallus varius* for dissection and study.

LITERATURE CITED

- AMADON, D. 1966. Avian plumages and molts. *Condor* 68:263-278.
- BEEBE, W. 1918-1922. A monograph of the Pheasants. Vols. I-IV. H. F. and G. Witherby, London.
- DANFORTH, C. H. 1958. *Gallus sonneratii* and the domestic fowl. *J. Hered.* 49:167-169.
- DE BEER, G. 1954. *Archeopteryx lithographica*. British Museum (Nat. Hist.). London.
- DELACOUR, J. 1951. The Pheasants of the world. J. C. Harrison, Country Life, London; Scribner, New York.
- DOMM, L. V. 1927. New experiments on ovariectomy and the problem of sex inversion in the fowl. *J. Exptl. Zool.* 48:31-173.
- DOMM, L. V. 1929. The effects of bilateral ovariectomy in the Brown Leghorn fowl. *Biol. Bull.* 56:459-497.
- GOODALE, H. D. 1916. Gonadectomy in relationship to the secondary sexual characteristics of some domestic birds. *Publ. Carneg. Inst.* (234), Wash., D.C.
- HUMPHREY, P. S., and K. C. PARKES. 1959. An approach to the study of molts and plumages. *Auk* 76:1-31.
- KIMBALL, E. 1954. Red-breasted mutation in *Gallus gallus*. *Poultry Sci.* 33:871.
- KIMBALL, E. 1958. Eclipse plumage in *Gallus*. *Poultry Sci.* 37:733-734.
- KIMBALL, E. 1959. Gray junglecock spangles. *Poultry Sci.* 38:240-241.
- LOTSY, J. P., and K. KUIPER. 1924. A preliminary statement of the results of Mr. Houwink's experiments concerning the origin of some domestic animals. *Genetica* 6:221-227.
- LOWE, P. R. 1944. An analysis of the characters of *Archeopteryx* and *Archaeornis*: Were they reptiles or birds? *Ibis* 86:517-543.
- MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York.
- MOREJOHN, G. V. 1953. A gene for yellowish-white down in the Red Junglefowl. *J. Hered.* 44:46-52.
- MOREJOHN, G. V. 1955. Plumage color allelism in the Red Junglefowl and related domestic forms. *Genetics* 40:519-530.
- MOREJOHN, G. V. 1966. Variation in the syrinx of the fowl. *Poultry Sci.* 45:33-39.
- MOREJOHN, G. V., and R. E. GENELLY. 1961. Plumage differentiation in normal and sex-anomalous Ring-necked Pheasants in response to gonadal hormone implants. *Condor* 63:101-110.
- SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *Condor* 59:166-191.
- STEAD, E. F. 1938a. "Eclipse plumage" possibly a universal factor in the sequence of moult in ducks. *Trans. Roy. Soc., New Zealand* 68:102-104.
- STEAD, E. F. 1938b. Further observations on the moult in the duck family. *Trans. Roy. Soc., New Zealand* 68:105-106.
- SWETOSAROW, E., and G. STREICH. 1937. Die experimentelle Analyse des Geschlechts und Saisondimorphismus in Gefieder der Enten. *Zool. Jahrb.* 58:225-240.
- VAN TYNE, J., and A. J. BERGER. 1959. Fundamentals of ornithology. John Wiley and Sons, Inc., New York.
- WALTON, A. 1939. On the eclipse of the Mallard (*Anas platyrhynchos platyrhynchos*). *J. Exptl. Biol.* 14:440-447.

Accepted for publication 13 March 1967.