PLUMAGE DEVELOPMENT AND MATURATION IN THE GREATER FLAMINGO *Phoenicopterus ruber roseus*

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ABSTRACT The Greater Flamingo is a long-lived species reaching maturity and breeding only after a period of years. Observations after fledging of birds ringed as chicks in the Camargue have revealed patterns of plumage succession which are presented here. During the first year there is little individual variation in the progression of the coloration of juvenile plumage and bare parts. Immature appearance, on the contrary, varies considerably between individuals, as does the age at which definitive plumage appears, normally after 4-6 years. There is a slight sexual dimorphism with females, identified by their smaller size, acquiring definitive plumage on average shortly before males. Causal and functional aspects of plumage development in the Greater Flamingo are discussed.

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INTRODUCTION

In many species of birds, definitive (adult) plumage is acquired only after several stages of juvenile and immature plumages (Lawton & Lawton 1985, Peterson 1991). This phenomenon has been reported for several long-lived aquatic species for which plumage coloration in juvenile and immature birds is distinctly different (duller) from that of adults. In albatrosses and gannets, for example, plumage maturation can last up to five or six years (Tickell 1969, Nelson 1978) or even go on throughout adult life (Nelson 1978, Weimerskirch *et al.* 1989). Such ontogenetic colour changes have been interpreted in different ways (Booth 1990). All five species of flamingos seem to show delayed plumage maturation, certainly the genus *Phoenicopterus* including the Lesser Flamingo *P. minor* (see Cramp & Simmons 1977, Ogilvie 1986).

In his study of the Caribbean Flamingo *P. ruber ruber* on Bonaire, Netherlands Antilles, Rooth (1965) suggested that several years are necessary before flamingos are fully coloured and can begin reproduction. He saw only fully coloured birds engaged in breeding.

The progressive development of the coloration of the plumage and bare parts of Greater Flamingos has been monitored as part of a study of the population ecology of this species in the Camargue, S. France, and elsewhere in the Mediterranean region. The species breeds in only a restricted number of localities throughout the western Palearctic region, (see Kahl 1975, Cramp & Simmons 1977). Observations of birds in juvenile plumage may indicate post-breeding dispersal and are of particular interest for the study of movements away from sites where no ringing has been carried out (Johnson 1989a).

METHODS

Data on the age of first breeding in flamingos are scarce and either concern birds in captivity (Studer-Thiersch 1975) or lack precision (Hoffmann 1957). It is only by marking large numbers of birds individually and subsequently searching for them in nesting colonies that such data can be obtained. Each year, since 1977 to date, a sample (from 518 to 721 individuals) of the Flamingo chicks raised in the Camargue, at the Etang du Fangassier, has been caught and ringed on the tibia with plastic leg bands engraved with an alphanumerical code (described in Johnson 1989b) which can be read in the field through a telescope at distances up to 400m (Johnson 1989a). These chicks are captured when in the nursery, or crèche, a short time before they

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take wing, generally in August, when the majority are about 2 - $2\frac{1}{2}$ months of age. Since the start of this marking programme these ringed birds have been regularly observed throughout the Mediterranean region and in West Africa by the team of ornithologists at the Tour du Valat Biological Station, and by amateurs.

At the beginning of this study detailed notes were taken whenever possible (birds standing at fairly close range and in good light) on the coloration of the plumage and bare parts of these individuals of known age and origin. After 5 years, 19 different plumages had been described (Johnson 1983). However, the differences between some of these were so slight (and insignificant) that only the 9 most distinct and most frequently recorded were retained and are presented here (Fig. 1). The others were considered as variations of these and grouped with the one of the nine which they most closely resembled. The data set was enhanced by the inclusion of 155 ringed birds of eight age classes (0.5 to 7.5 years), the corpses of which were collected in January 1985 during a period of severely cold weather.

In 1982, when many of the first cohort of ringed birds were in adult plumage, observations were begun at the natal colony to see if any individuals were attempting to breed. The following year, a tower hide was built 70 m. from the nesting colony in the Camargue and this has been used by observers permanently during the whole of the breeding season since 1983. The observers' main activity has always been to ascertain which ringed birds were breeding.

Sex-related asynchrony in plumage development was assessed by comparing the proportion of different plumage categories across age classes between males and females. We also compared the sex ratio of the youngest birds recorded in adult plumage as well as the sex ratio of breeding birds displaying traces of juvenile plumage. Differences were considered significant at the 5% level.

RESULTS

Plumage: the different plumages observed in the field are illustrated in Figure 1 and described in brief in Table 1. The age and period during which these are worn are given in Figure 2. Each individual appears only once in a particular category, the first time it is recorded in that plumage.

Juveniles lack pink colouring in their plumage, other than on their under wing-coverts, and can be recognised until they are almost one year old. At 11 months they begin to acquire a pale pink upper wing panel and soon after this the legs and bill also turn pinkish-grey.

The development of immature plumage is extremely variable in time and in a group of birds of the same age the tones of pink and grey may be quite diversified. Likewise, in July for example, a flamingo in plumage "E" is most likely to be two years of age but could in extreme cases still be in its first year, or in its third year.

Adult plumage is acquired at the very earliest at 30 months but by most birds not until they are 4 years of age. The body, scapulars and tail are then wholly white with a pinkish tinge. The primaries and secondaries are black and the upper and under wing-coverts crimson. The tip of the bill is also black and there is a well defined line separating this from the base which, like the legs, is a deep pink. The pattern of the upper edge of the black tip on the pink base differs amongst individuals and when seen face on at close range can be used as an identification feature, albeit for studying relatively small numbers of birds, as has been shown for example with Bewick's Swans *Cygnus columbianus bewickii* (Evans 1977). The iris is yellow.

The amount of pink coloration, noticeable particularly on the head and neck, varies greatly amongst individuals, not in relation to age (some birds have a very pink head when otherwise still in immature plumage) but possibly according to diet and an individual's capacity to assimilate carotenes for pigmentation or, as indicated by Allen (1956) to the amount of fat or oil in the feathers. This bright coloration can appear as early as September, following the autumn moult, but is most often observed between November and February, disappearing in March-April. Eighty-eight ringed individuals have been seen in this bright attire, three of them during five different winters, indicating that it may

Fig. 1. The sequence of plumages and coloration of bare parts from juvenile through to definitive appearance in the Greater Flamingo (A, B, C, juveniles; D, E, F, G, immatures; H, I, adults).

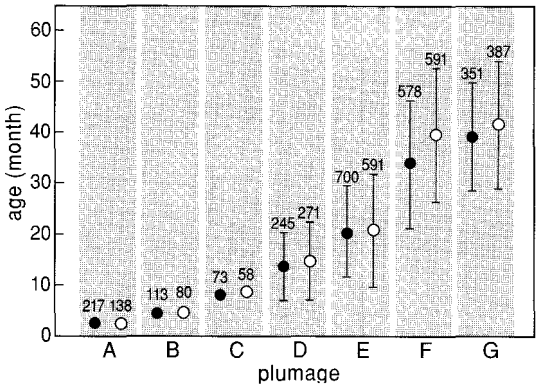

Fig. 2. Comparative development of juvenile (A-C) and immature (D-G) plumages between males and females in the Greater Flamingo. Vertical bars show standard deviations.

be genetical variation and consistent in some birds. Presumably, it is the new feathers of some individuals which are brightly coloured as they grow and when fresh, but soon afterwards fade. Indeed the fact that they fade quite rapidly is said to have saved flamingos from exploitation in former times by the millinery trade (Allen 1956). There is otherwise no seasonal variation in plumage, nor are there differences between sexes, which can be distinguished in the field only by their difference in size.

There is however a slight difference in plumage development between the two sexes. Plumage development is synchronous between males and females until the age of 12 months (plumages A-C). Then, until the age of 85 months, there is a significantly higher proportion of females still displaying sub-adult plumages (χ^2-test, $p < 0.05$). This difference is reversed for birds between 97 and 108 months in which more males are still lacking full adult plumage (χ^2-test, $p < 0.05$). There is no longer a significant difference between males and females in the proportions of the various plumage categories after the age of 120 months.

Of the 24 marked individuals of known sex which acquired full plumage before the age of 36 months, 21 were males and only 3 females (binomial test $p < 0.05$). Of the 24 individuals of known sex which still exhibited traces of immature attire at the age of 5 years, there was no significant differ-

Table 1. A brief description of the development of the coloration of plumage and bare parts in the Greater Flamingo.

1. Grey base to bill. Legs black or grey with darker joints. Back and wings mottled grey-brown but paler on lower underparts.
2. Base of bill and legs as above. Body off-white with mottled back, grey on nape.
3. Base of bill and legs as above. Body white with a little grey on nape.
4. Base of bill grey or pinkish-grey. Legs grey with darker joints. Wing panel partly or entirely pale pink.
5. Base of bill pale greyish-pink. Legs greyish-pink and scaley, the joints still darker. Body still white. The wing reddish-pink.
6. Base of bill pale pink. Legs pale pink, uniform or with joints slightly darker. Body white but possibly a little grey on nape. Wing crimson.
7. Base of bill and legs pink but one feature of immature plumage retained; either base of bill or legs still pale pink, leg joints still darker than rest of legs or there is a little grey still on nape.
8. Base of bill and legs uniformly deep pink. Body pinkish-white.
9. Base of bill and legs deep vermillion pink. Body with pinkish hue, most intense on head and neck.

ence between males and females. Of the 37 marked birds seen breeding whilst still displaying some feature of immature coloration, there were 17 males and 20 females (binomial test n.s.), one of the latter still having greyish-coloured legs at the age of 14 years.

DISCUSSION

Causal and functional accounts

The development and maturation of plumage in flamingos according to this study falls in line with morphological (ontogenetic) colour changes described by Booth (1990), resulting from synthesis of pigments. The interpretation of ontogenetic colour changes involves both causal and functional explanations. On the one hand, the progressive acquisition of definitive plumage corresponds to several physiological mechanisms, while on the other hand, delayed plumage acquisition might have an adaptive value or be the result of developmental constraints.

The red and pink coloration of the flamingo's plumage and bare parts reflects rich sources of carotenoids in their natural diet, and a great efficiency in their metabolic processing of these labile compounds (Fox 1975). The mechanisms which bring about feather colour change in flamingos are complex (Fox 1975) and go beyond the scope of the present paper. It is nevertheless useful to recall that different physiological factors can be responsible for the progressive development of plumage. It is also possible that as a bird grows, other physiological processes take priority over the synthesis of certain pigments. The change of plumage colour over a period of time may correspond with a change of diet although we have no direct evidence to support this assumption. It may also be that the synthesis of pigment is only possible after accumulation of certain substances which may take several years.

Flamingo chicks move into a nursery when they are around 2-3 weeks of age. They are then covered in a dull grey down which is replaced progressively by the first plumage, itself cryptic. Although the main defense system against predators may be the sheer isolation of many of the flamingo's breeding sites, the value of cryptic coloration and creching as protection against predators is undoubtedly important (see Baker & Parker 1979). Another important aspect of delayed plumage maturation is that it may reduce aggression by adults towards juveniles. However, there is poor evidence to support this hypothesis in flamingos. Bildstein *et. al.* (1991) observed that juveniles of Caribbean Flamingo *P. r. ruber* were in fact more likely to be involved in aggressive encounters and to be the recipients of aggression than were adults. Although we didn't attempt to quantify agonistic events in relation to age, we regularly observed in the Camargue a spatial segregation of age classes on feeding grounds throughout the year, suggesting that birds in immature plumage might avoid direct interference with adults.

Geographical variation in plumage coloration

The Greater Flamingo of the Old World is paler than *P. r. ruber* of the Caribbean region and this agrees with Gloger's (1833) Rule that species are more brightly coloured in hotter climates. There is variation of the coloration of plumage and bare parts within the range of the Greater Flamingo. During the capture of chicks for ringing many of those at Fuente de Piedra (Andalucia) 1000 km to the south of the Camargue, have a red coloration of the under wing-coverts, whereas the birds in the Camargue are generally pale pink at the same age. In South Africa, Uys *et al.* (1963) state that at the age of 39 days chicks have a pinkish tinge to their mandibles and at 50 days have pinkish bills. The primaries also have a pinkish tinge. Even more striking, Berry & Berry (1976) state that the bill colour (at the base) of the chicks they hand-reared in Etosha National Park, changed from coral red to blue-grey at 11 weeks, later became off-white and turned pink at six months of age. Leg colour changed slowly from deep pink through dull black to off-white when the chicks were nine to 12 weeks old, except for the tibio-tarsal joint which remained darker until their release after six months. It cannot be excluded that these hand-reared birds may have showed an excess of normal pigment in the plum-

age (Harrison in Campbell & Lack 1975). Such a difference in coloration between the Camargue and southern Africa may well be the result of a differing diet between the two sites.

Comparison with other species

Prolonged plumage maturation has been studied in several non passerine bird species (Nelson 1978, Johnsgard 1983, Weimerkisch *et al.* 1989) with which some comparisons can be drawn. The progressive temporal development of plumage coloration in the Greater Flamingo shows broad similarities with that of the Gannet *Sula bassana*, another species where the adult plumage is simple, but that of the many immature stages is not (Nelson 1978). Similarities are:

- At 24 or 36 months after hatching, the bird may be like another a year younger or a year older.
- Just under half of the four year old birds look adult.
- It is unusual to find any 5 year old birds with any immature plumage.
- Some individuals exceptionally keep some feature of their immature appearance much later in life, in the case of the flamingo greyish tibio-tarsal joints until 7 years of age.
- They usually do not breed until they are in at least their fifth year.

In contrast, most of the Cranes *Grus* spp., another group of long-lived wading birds similar in size to flamingos, seem to acquire their definitive appearance in their first or second year, although they do not breed until they are several years of age (Johnsgard 1983).

Delayed plumage maturation and deferred sexual maturity

Until recently, discussion of the delayed acquisition of fully adult plumage was considered only as a corollary to discussions of deferred breeding (Lawton & Lawton 1986). There are, however, several instances showing that the retention of morphologically sub-adult plumage by reproductively mature animals is not uncommon in birds. Generally, breeding by morphologically sub-adult birds occurs when, for whatever reason, populations are temporarily released from the effects of saturation (Blus & Keahey 1978) or when food becomes super-abundant (Pitelka *et al.* 1955). Although the vast majority of flamingos already have their definitive appearance when they breed for the first time, this seems not to be a prerequisite since we have exceptionally recorded birds breeding which had retained some trait of their immature appearance, with no difference between sexes. According to our present knowledge breeding by morphologically sub-adult flamingos has not been reported before. We had however no evidence that the phenomenon is attached to particular environmental conditions such as an increase in food availability or a decrease in the density of breeders. It is clear however that definitive morphological appearance and sexual maturity are not reached simultaneously in the Greater Flamingo. Although our analysis reveals a slight asymmetry in plumage development between males and females, we found no difference between the two sexes in the propensity to breed in immature plumage. However, costs associated with breeding in immature plumage have not been evaluated within this study and might be different for males and females.

Some comments on moult

No detailed study into the timing and manner in which flamingos moult has been carried out by us since this would require capturing large numbers of birds and is not feasible with this species. However, we have observed that the manner in which flamingos moult is very variable. In the Camargue, both progressive and simultaneous moult have been recorded. The former is the most frequent since it is not every year that flightless adults are observed in two of the larger lagoons intensely used for feeding. It is doubtful if any birds having lost the capacity to fly would be raising chicks, certainly not those in one of the two lagoons in question, but they are more likely to be non-breeders or failed breeders. At Lake Uromiyeh (Iran) and in East Africa, flamingos undergo a simultaneous moult of their remiges and become flightless for some

time. Brown (1975) suggested that the birds may even be able to control their moult because those breeding at Lake Magadi in Kenya, where they have to fly elsewhere to feed, did not become flightless.

Stresseman & Stresseman (1966) reported that flamingos moult simultaneously only once every two years and suggested that successful breeding would only take place in years in which they are not moulting. However, this was based on sparse information on captive individuals. We actually found no evidence for such a phenomenon when observing free ranging flamingos in the Camargue. Indeed, we observed many ringed birds successfully breeding several (up to four) years in succession, suggesting that moult of flight feathers is a post breeding event. Further, we found no evidence for moult cycles as data points show no clustered distribution, but instead tend to be normally distributed around the mean (Fig. 2).

A guide to assessing the age of flamingos

The colour plate (Fig. 1) is a guide to assessing the age of flamingos according to their appearance. Although the majority of flamingos occurring in the western Mediterranean will be of French, Spanish or Tunisian origin, Johnson (1989a) has shown that some birds from Mauritania move north to the Mediterranean during post-fledging dispersal (observations based on the sightings of birds in juvenile plumage). The breeding season can be much longer in West Africa with juveniles taking wing from two months earlier to two months later than in the Mediterranean region, from April through to October. This must be borne in mind when using appearance as a cue to ageing flamingos.

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SAMENVATTING

Tot voor kort was er weinig bekend over de ontwikkeling van het verenkleed en de geslachtsrijpheid bij de Flamingo. De bestaande kennis berustte voornamelijk op waarnemingen aan dieren in gevangenschap. Dankzij uitgebreid ringonderzoek aan jongen in de Camargue is meer bekend geworden over dit proces bij in het wild levende Flamingo's. Sinds 1977 is gewerkt aan individueel gemerkte vogels met gecodeerde plastic ringen. Hierover wordt in dit artikel gerapporteerd.

Flamingo's bereiken hoge leeftijden (20-40 jaar) en komen pas tot voortplanting op een leeftijd van 4-6 jaar, waarop zij tevens hun definitieve verenkleed krijgen. Daarvóór verandert hun verenkleed, en ook de kleur van hun snavel en poten (Fig. 1 & Tabel 1). Gedurende het eerste jaar is er weinig individuele variatie. In de subadulte stadia is dat wel het geval (Fig. 2). Wijfjes, die kleiner zijn dan mannetjes, krijgen hun definitieve verenkleed gemiddeld vroeger dan de mannetjes.

De trage – in vergelijking met andere vogelsoorten – ontwikkeling van het verenkleed wordt in verband gebracht met voedsel, pigmenten en met bescherming tegen predatoren en agressie van soortgenoten. Het bereiken van geslachtsrijpheid kan plaatsvinden voordat het definitieve verenkleed verschijnt, maar de voortplanting wordt gewoonlijk uitgesteld totdat het dier niet meer van ouderen kan worden onderscheiden. - Jan Rooth