PLUMAGE AND SEXUAL MATURATION IN THE GREAT FRIGATEBIRD *FREGATA MINOR* IN THE GALAPAGOS ISLANDS

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SUMMARY

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The adaptive significance of distinctive immature plumages and protracted sexual and plumage maturation in birds remains controversial. This study aimed to establish the pattern of plumage maturation and the age at first breeding in the Great Frigatebird *Fregata minor* in the Galapagos Islands. We found that Great Frigatebirds attain full adult plumage at eight to nine years for females and 10 to 11 years for males and that they rarely attempted to breed before acquiring full adult plumage. The younger males succeeded only at attracting a mate, and males and females both bred at the age of nine years when their plumage was nearly completely adult. Although sexual maturity was reached as early as nine years, strong competition for nest-sites may further delay first reproduction. We discuss our findings in light of the several hypotheses for explaining delayed plumage maturation in birds, concluding that slow sexual and plumage maturation in the Great Frigatebird, and perhaps among all frigatebirds, may result from moult energetic constraints during the subadult stage. Therefore, slow plumage maturation in frigatebirds may not be an adaptation for distinctive subadult plumage *per se,* as is often suggested for birds.

Key words: Frigatebirds, delayed plumage maturation, sexual maturation, immature plumage, moult

INTRODUCTION

The five species of frigatebirds (Fregatidae) are a group of closely related tropical seabirds that are very similar in behaviour, breeding and foraging ecology (Diamond 1973; Nelson 1976; Coello *et al.* 1977; Valle 1986; Schreiber & Schreiber 1988; Reville 1988, 1991; Kennedy & Spencer 2004). Casual information suggests that frigatebirds display a variety of immature plumages and take several years to mature sexually and to acquire full adult plumage (Diamond 1975; Nelson 1976, 1983; Harrison 1983; Valle 1986). However, no study has established clearly the pattern of plumage development and the age of first breeding for any species of frigatebird, nor is there an explanation for the extended period of immature appearance nor for the adaptive significance of distinctive immature plumages in frigatebirds.

Research on the evolution of distinctive subadult plumages in birds has focused on the adaptive significance of delayed plumage maturation in passerine birds (Rohwer 1975, Rohwer *et al.* 1980, Proctor-Grey & Holmes 1981, Studd & Robertson 1985, Hill 1988, Rohwer & Butcher 1988, Moller 1989, Grant 1990) and shorebirds (Chu 1994). However, nonpasserine birds, particularly marine birds that have evolved a rather distinctive set of life-history traits (Nelson 1983, Snow & Nelson 1984, Croxall 1987), have remained largely neglected.

Several hypotheses have been proposed for the evolution of distinctive subadult plumages and delayed plumage maturation. The cryptic hypothesis suggests that cryptic immature plumage enhances survival by reducing conspicuousness to predators and avoiding conspecific aggressive encounters (Selander 1965, 1972; Procter-Gray & Holmes 1981; Rohwer *et al.* 1983). The mimetic (female mimicry) hypothesis states that by mimicking a female's plumage, immature males are less exposed to attacks from adult males and may benefit from enhanced access to resources such as food and mates (see Rohwer *et al.* 1980). The status-signalling hypothesis states that by displaying a distinctive plumage, immature birds signal their subordinate status and benefit by reducing aggression from adults (Rohwer 1975, Lyon & Montgomerie 1986, Rohwer & Butcher 1988). The breeding-threshold hypothesis, which builds upon life-history models that emphasize trade-offs between survival and reproduction to maximize lifetime reproductive success, suggests that sexually mature young birds delay first breeding to enhance survival (Studd & Robertson 1985, Montgomerie & Lyon 1986). Finally, the moult-constraint hypothesis, which is consistent with a more general breeding threshold, argues that subadult plumages are nonadaptive and are the result of energy limitations that prevent young birds going through a complete post-juvenile moult and acquiring adult plumage (Rohwer *et al.* 1983, Rohwer 1986, Rohwer & Butcher 1988).

We conducted a long-term study on a marked population of Great Frigatebirds *Fregata minor* in the Galapagos Islands, Ecuador. Our study aimed to establish the pattern of plumage maturation in frigatebirds and the age at first breeding for this species, while addressing the question of the evolution of protracted plumage maturation and the adaptive significance of displaying distinctive immature plumages.

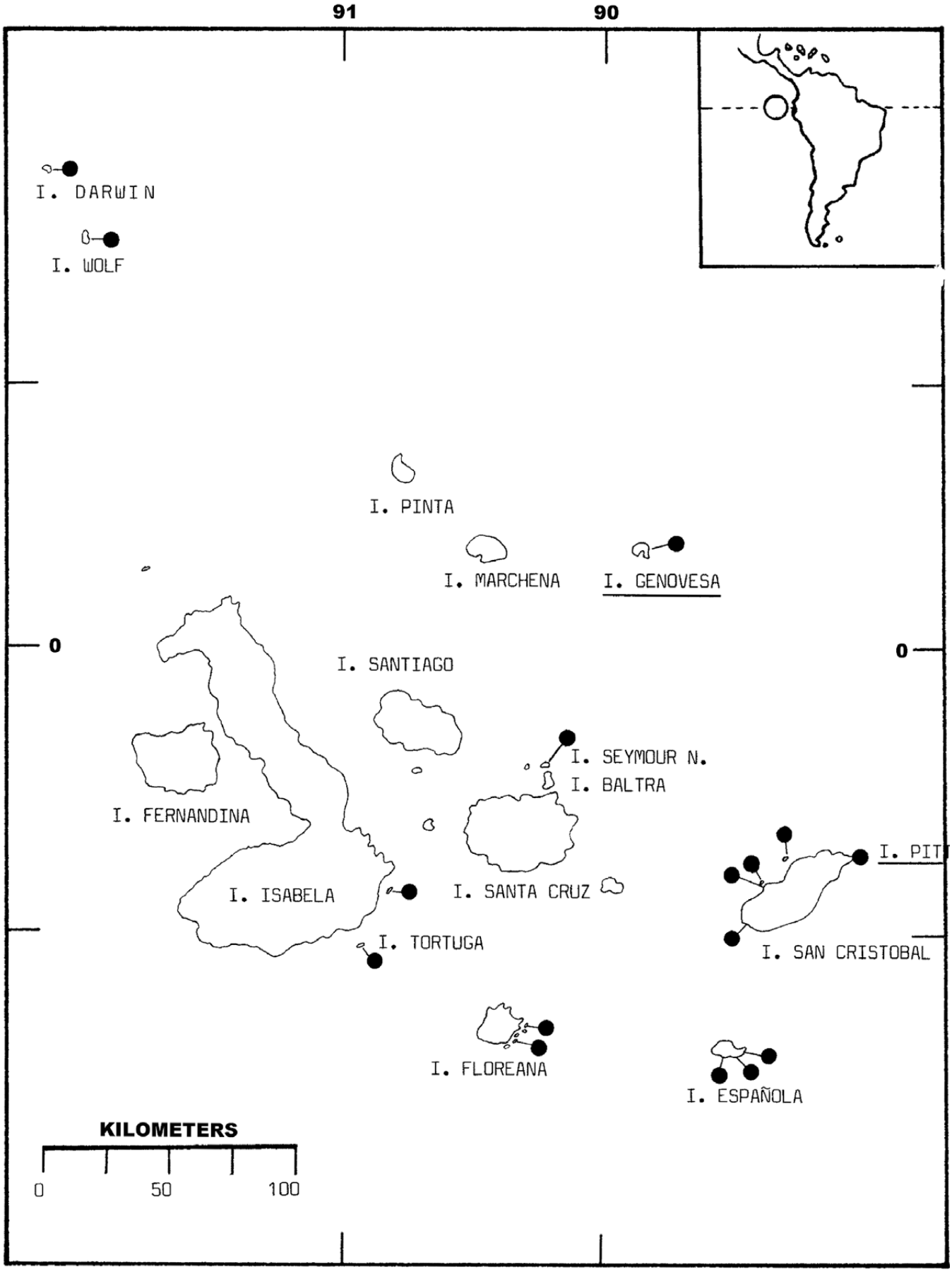

Fig. 1. The distribution of breeding colonies of Great Frigatebirds in the Galapagos Islands, showing the study sites at Darwin Bay (Genovesa Island) and Pitt Islet (off San Cristóbal Island) (modified from Valle 1986).

STUDY AREA AND METHODS

We studied Great Frigatebirds on the Galapagos Islands at Darwin Bay, the largest breeding colony on Genovesa (Tower) Island, and at Pitt Islet near San Cristóbal Island (Fig. 1) where T. de Vries and coworkers (unpubl. data) had banded 294 Great Frigatebirds as nestlings or fledglings (dependent juveniles hatched the previous calendar year) from 1975 to 1983. Darwin Bay has an annual breeding population of about 200 pairs of Great Frigatebirds that is relatively isolated from the other breeding groups scattered through the 17 km² of the island (for a detailed description of Genovesa, see Grant & Grant 1980). Pitt Islet is a 0.5-ha basaltic rock about 0.4 km off the northwest coast of San Cristóbal Island, with an annual breeding population of about 40 pairs.

From July 1983 to November 1984, we conducted systematic searches for banded birds at the two main study colonies. During that period, and occasionally thereafter, we also searched for banded birds at least once at each of the breeding colonies of Great Frigatebirds within the Galapagos Islands. Frigatebirds were captured by hand or by placing a light bamboo pole between their wings when they were sitting at the nest, sitting on low bushes or roosting on cliffs. For each captured bird, we recorded sex, morphometrics and the moulting status of the flight feathers (primaries and rectrices). Sex was determined by bill size (males ≤ 100 mm ≥ females—Diamond 1975, Coello *et al.* 1977). For 70 frigatebirds in immature plumage, including 12 of known age, we made a sketch of the body plumage and described it in detail.

We quantified the plumage stage of immature frigatebirds by scoring the plumage of the following body areas: (1) head, including crown, nape and sides of the head; (2) neck, including chin, throat hindneck and foreneck; (3) breast; and (4) belly, including sides, flanks and central belly. The score for each area was assigned according to the percentage of white or rusty juvenile plumage replaced by black, as follows:

- 0: completely white or rusty, the typical juvenile plumages at the time frigatebirds fledge
- 1: ≤25% black
- 2: 26%–50% black
- 3: 51%–75% black
- 4: 76%–99% black
- 5: 100% black

The total plumage-score (0–20) for each bird was computed as the sum of the four body area scores. We constructed the basic pattern of plumage maturation by regressing plumages scores against age and by sequentially arranging the plumage sketches of the 12 birds of known age. Then the sketches of 58 other immature birds of unknown age were visually fitted, according to their total plumage score, within the basic pattern to produce a scheme of plumage change. We used this visual scheme to derive a basic pattern of plumage maturation.

RESULTS

From July 1983 to November 1984, we captured more than 5000 Great Frigatebirds in adult plumage and 320 in immature plumage (Table 1). Among the captured birds we found 12 (4.1%) of the 294 frigatebirds banded as nestlings or fledglings from 1975 to 1983 (Table 2). Three of the latter birds (one female and two males) were nine years of age, had a nearly or already full adult plumage, and corresponded to nestlings from the 1974 cohort banded at Pitt Islet (Table 3). The other nine birds, whose age ranged from one and a half to six years, displayed a variety of immature plumages.

TABLE 1
Great Frigatebirds in adult and immature plumage captured between July 1983 and November 1984 while searching for birds banded as nestlings or dependent fledged juveniles (nestlings of the previous calendar year) from 1975 to 1983 in the Galapagos Islands

	Genovesa Island		Pitt Islet	Other islands	Total	Recapture of birds banded as juveniles
	Darwin Bay	Other colonies				
Adult plumage	3680	1227	38	369	5314	3
Adults (BR)	450	1040	38	347	1875	3
Adults (NB)	3230 [a]	187 [a]	0	22	3439	0
Immature plumage	150	75	70	25	320	9
Total	3830	1302	108	394	5634	12

[a]Estimate based on the total number of captures (Darwin Bay = 3800; other colonies = 220) during eight two-week to three-week capturing sessions and assuming a recapture rate of 15% among nonbreeding adult Great Frigatebirds (C.A. Valle unpubl. data).

TABLE 2
Great Frigatebirds banded (B) as nestlings or dependent fledged juveniles in the Galapagos Islands from 1975 to 1983 and the number recaptured (R) among more than 5000 birds in adult and 320 in immature plumage captured throughout the Galapagos Islands between July 1983 and November 1984 (see Table 1)

Year of hatching	Genovesa		Pitt Islet		Total	
	B	R	B	R	B	R
1974	11	0	–	–	11	0
1975	–	–	46	3	46	3
1976	7	0	–	–	7	0
1977	42	1	–	–	42	1
1978	7	0	–	–	7	0
1979	43	0	22	2	65	2
1980	1	0	–	–	1	0
1981	51	4	–	–	51	4
1982	40 [a]	1	24	1	88	2
TOTAL	202	6	92	6	294	12

[a] The number of juveniles banded in 1983 (cohort born in 1982) was 64. However, 20 of then died at the nest site, presumably from starvation because of the impact of El Niño 1982/1983 (Hernández & de Vries 1985, Valle 1985, Valle *et al.* 1987).

Adult and juvenile plumage patterns

The plumage description of adult and immature (juvenile and subadult) Great Frigatebirds that follows is based on our own observations, and adds to general descriptions to be found elsewhere (Nelson 1976, Harrison 1983).

Adult Great Frigatebirds are sexually dimorphic in both size and plumage colour. Males are smaller than females and are entirely black, with a tuft of longer lanceolate green-iridescent feathers on their back and scapula region that turns brighter during the mating season and early in the breeding cycle. Males tending fledged juveniles (six months or older) have duller, browner overall plumage and fewer iridescent feathers. A similar pattern is also reported for Great Frigatebirds in the Hawaiian Archipelago (Dearborn & Anders in press, D.C. Dearborn unpubl. data). A brown wing bar and small brown dots on the axils are diagnostic features that, in the Galapagos Islands, allow us to distinguish the Great Frigatebirds from the larger and more shiny-black males of Magnificent Frigatebirds *F. magnificens.* Females are mostly dull black, have a white breast, greyish-white chin and throat, and lack the longer lanceolate feathers on their back. Orbital rings are black in males and red in females.

Juveniles are sexually monomorphic in plumage, typically characterized by a white—although variably rust-stained—head, neck, breast and belly. The rest of the body plumage is dull black as in adult females, but displays a noticeable whitish-brown wing-bar. The juvenile plumage is fully acquired (i.e. all down has been replaced by feathers) when birds are five and a half to six months old. The orbital ring is green-blue in all birds in juvenile plumage.

We recognize two juvenile plumage-stages. Juvenile I stage, lasting up to 1.5 years of age, is characterized by heavily rust-stained white plumage areas and by a diffuse reddish-brown breast-belt noticeable at the time of fledging. The rust colour at this age is a diagnostic feature that distinguishes juvenile Great Frigatebirds from the unstained, white-headed juvenile Magnificent Frigatebirds. Juvenile II stage, lasting up to two and a half to three years of age, has a white-headed appearance, because the rust colour has largely faded from the head and neck.

Subadult plumages and plumage maturation

The derived pattern of plumage maturation (see "Methods") based primarily on 12 birds of known age (Table 3) showed that, in the Great Frigatebird, plumage maturation is clearly age-related (Fig. 2), displaying a continuous sequence of transitional plumages rather than truly distinctive subadult plumage stages. Fig. 3 depicts juvenile, adult and five sequential subadult plumage stages that summarize the entire pattern of plumage maturation.

The first changes on the typical juvenile plumage (juvenile I) involve a gradual fading of rust-coloured feathers of head and neck, starting at the age of one and a half years. These changes on the juvenile appearance become noticeable in the field when birds are two and a half to three years old, when much of the rust colour has disappeared and almost imperceptible black speckles appear around the eyes. Although most of the rust colour usually disappears by the end of the third year, some individuals, particularly females, may retain traces of rust colour on the breast until age eight or nine years.

TABLE 3
Plumage description of the 12 immature (juvenile and subadult) Great Frigatebirds recaptured between July 1983 and November 1984 that were previously banded as nestlings or juveniles in the Galapagos Islands

Age (years)	Sex	Total plumage score	Body plumage description
1.67	M	0	Typical juvenile plumage (see plumage description)
1.70	M	0	Typical juvenile plumage (moult of primary feathers started)
1.75	F	0	Typical juvenile plumage (moult of primary feathers started)
2.10	M	0	Typical juvenile plumage (moult of primary feathers started)
2.10	M	0	Typical juvenile plumage (moult of primary feathers started)
2.40	M	2	Typical juvenile plumage except for less rust colouration and the presence of a few faint, almost inconspicuous, black feathers scattered along the supercilliary region and hind belly (around cloacae); orbital ring green-blue like typical juveniles
4.75	F	3	Head white-spotted with black around the eyes, forehead, and eye line; neck and breast completely white and white belly with a few scattered black spots around the cloacae; orbital ring aqua-blue faintly spotted with red
5.17	M	5	Head white, densely spotted with black around the eyes, forehead and eye line; neck and breast completely white and belly about 50% black with mottled appearance; orbital ring green-blue spotted with tiny black dots covering about 20%
5.75	F	9	Head white, black ring around the eyes, black forehead and black eye line extending throughout sides of neck, giving an osprey-like appearance; neck white with black on sides, breast completely white and belly almost completely filled with black; orbital ring aqua-blue about 15% covered with red
9.08	F	14	Full adult plumage with head completely black and neck mostly black except for white chin and throat; white breast and belly completely black; orbital ring completely red
9.10	M	17	Head, neck, including chin and throat, and belly completely black; breast white sparsely spotted with black; orbital ring completely black
9.20	M	19	Plumage almost completely black except for whitish breast densely spotted with black; orbital ring completely black

Data for Great Frigatebirds on Tern Island, Hawaii, are consistent with the pattern we describe here, showing one young-adult female aged eight years old with tan breast compared with one seven-year-old bird that had already achieved a completely white breast (Table 4).

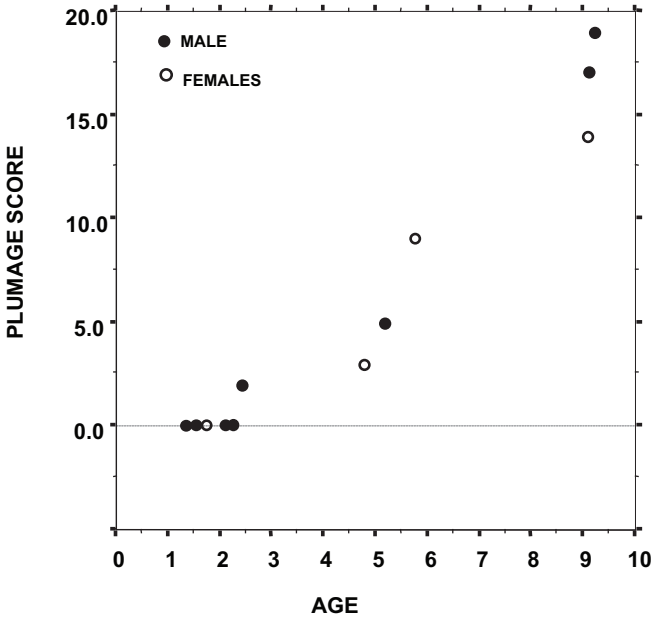

Fig. 2. The body plumage scores of 12 immature Great Frigatebirds was highly correlated with age (corrected Spearman $\rho = 0.966$, $P < 0.01$, $n = 12$).

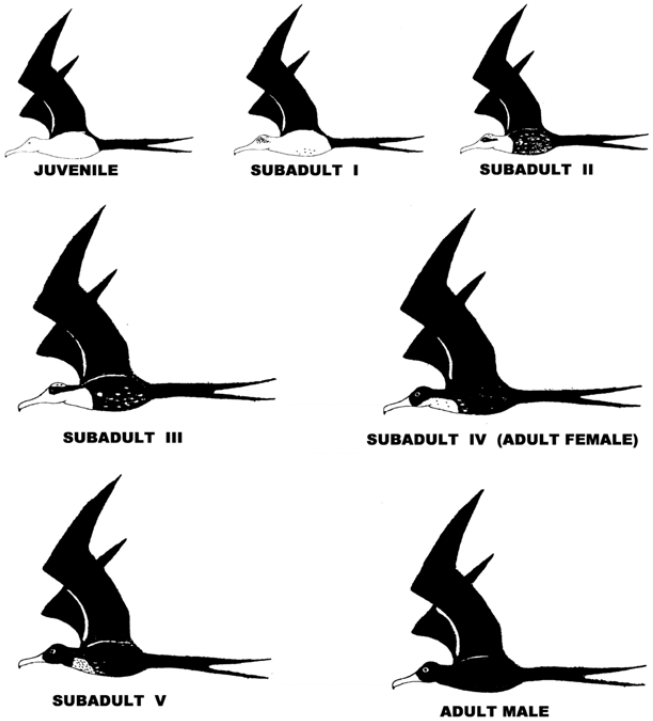

Fig. 3. The juvenile, adult and the five subadult plumage stages that summarize the pattern of plumage maturation in the Great Frigatebird. Sketches are based on 12 immature birds of known age recaptured during this study (see Table 3). The unstained juvenile at stage II is not depicted.

Replacement of the white juvenile plumage by black feathers occurs throughout two plumage regions, beginning at about the same time on the head, around the eyes and on the hind ventral area, usually around the cloaca. The head moult progresses downward with the head and then the neck changing to black. On the other hand, belly moult progresses forward, with the breast area the last to turn black. Females reach full adult plumage at subadult stage IV (age of eight to nine years), but at that stage, subadult males display a plumage that resembles that of an adult female Great (throat whitish) or a female Magnificent (throat and foreneck blackish) Frigatebird (Fig. 3). The male's breast turns speckled blackish after the bird reaches the age of nine years; thereafter, the moult to greyish, brown or black feathers progresses concentrically. Males that are about 10 years old frequently show a circular or horseshoe-shaped whitish spot in the centre of the breast and attain full adult plumage (breast completely black) when they are about 10–11 years old.

The breast plumage of male Great Frigatebirds in the Hawaiian Archipelago (Table 4) also agrees with the pattern found in the Galapagos Islands and further suggests that some males may retain traces of white feathers on the breast up to 13 years of age.

TABLE 4
Plumage description (breast colour) of 14 male and four female Great Frigatebirds[a] recaptured during three field seasons in 1998, 2000 and 2005 on Tern Island, French Frigate Shoals, Northwestern Hawaii Islands (D.C. Dearborn unpubl. data)

Age (years)	Breast colour	Capture (calendar year)
Males		
>30	Black, brown or grey	1998–2005
15	Black	2005
15	Blackish brown	2005
15	Greyish black	2005
14	Blackish brown	2005
14	Greyish black	2005
13	Black	2000
13	Greyish white	2000
10	White mottled with white and grey	2000
10	Whitish	1998
10	Whitish	1998
9	Greyish white	2005
9	Greyish white	2000
9	Mostly solid white	1998
7	Mostly solid white	1998
Females		
35	White	1998
9	White	1998
8	Tan	1998
7	White	1998

[a] Birds were banded as nestlings by the United States Fish and Wildlife Service in the 1960s and from 1988 to 1991.

The male's iridescent lanceolate feathers on the back and scapula regions become noticeable at the age of five years, reach about half their final length and number at the age of six to seven years and reach their full length at eight to nine years.

The green-blue juvenile orbital ring becomes spotted with black at the age of three to four years and turns completely black (males) or red (females) at an age of seven to eight years. Among the 70 immature males, we found eight males younger than five years displaying blue orbital rings spotted with red, five birds aged six to seven years with orbital rings completely red (as for females), and four older than seven years with orbital rings showing a mixture of red and black spots. However, we found no males in full adult plumage possessing red orbital rings. We therefore infer that possession of red orbital rings is only a transitional stage displayed by some males when about six to seven years of age.

Plumage and age at sexual maturity

Three males of known age at Pitt Islet in 1984 were the first to be found breeding from a cohort of 43 chicks banded at the same locality in 1975. By then they were nine years old and already in full adult plumage except for a small whitish patch in the middle of the breast. Among the more than 800 breeding birds (i.e. attending nests with egg or chick) whose plumage was visually inspected (Table 5), we found no males in noticeably immature plumage. However, judging by a small whitish patch in the breast that was similar to that in nine-year-old males, about 4% (n = 823) of them were young adult breeding males.

Subadult males displaying plumage similar to that of six- to seven-year-old birds (a speckled crown, whitish breast and orange-red gular pouch), only rarely and unsuccessfully attempted courtship. We observed a single exceptional case of courtship by a male in unusually young plumage, with head and neck almost entirely white, displaying a small, not well distended orange pouch. A rare but similar observation was reported in Great Frigatebirds on Aldabra Atoll (see Diamond 1975) and has also occasionally been observed in Hawaii (D.C. Dearborn pers. comm.).

The only female from the cohort born at Pitt Islet in 1975 that we found breeding at the same place was nine years old and already had full adult plumage, although with a few rust-coloured feathers scattered over its white breast. We inspected the body plumage of more than a thousand females attending nests with eggs or chicks (Table 5), and found only two females with slight whitish crowns breeding while not yet in full adult plumage. However, as inferred from rust-coloured feathers on their breast, we considered that about 4% (n = 1068) of breeding females observed were also young adult breeders.

TABLE 5
Number (N) of breeding Great Frigatebirds whose plumage was visually inspected, and the percentage of young adults (birds with traces of rust-coloured or white feathers) found at several colonies in the Galapagos Islands between July 1983 and November 1984

Colony	Males		Females	
	N	%	N	%
Genovesa Island				
B. Darwin	218	(1.4)	232	(5.2)
Other colonies	430	(2.3)	610	(1.6)
Pitt Islet	15	(26.7)	23	(8.7)
North Seymour	160	(9.0)	198	(11.7)
San Cristóbal				
Playa Ochoa	—	—	5	(0.0)
Total	823	(3.8)	1068	(4.3)

DISCUSSION

Plumage maturation and age at first breeding

This study shows that plumage and sexual maturation in the Great Frigatebird are slow, gradual and correlated processes that are completed only when females are eight to nine and males 10 to 11 years of age or older. Males and females only rarely attempted to breed before attaining full adult plumage, and no male with noticeable immature plumage succeeded at attracting a mate.

Although sexual and plumage maturation coincide and Great Frigatebirds start attempting to breed at this stage, we expect that first reproduction may be even further delayed. A strong competition for preferred nest sites prevents part of the potential breeding population from mating every year (Valle 1986). Thus, the Great Frigatebird has a prebreeding period longer than that of most other seabirds. The only other seabirds with comparable slow plumage and sexual maturation are the large and pelagic albatrosses of the genus *Diomedea* that, on average, start breeding when 11–12 years of age (Tickell 1967), Weimerskirch & Jouventin 1987, Jouventin & Weimerskirch 1990).

The pattern of plumage maturation

Sequential immature plumages that are assumed to result from periodic moults have been reported in several long-lived birds with an extended prebreeding period, including birds of prey (Bortolotti 1984, McCullough 1989, Cabot & de Vries 2004) and seabirds such as albatrosses (Harris 1973; Prince *et al.* 1997; Harrison 1979, 1983; Weimerskirch & Jouventin 1987; Weimerskirch *et al.* 1989; Hyrenbach 2002), boobies and gannets (Nelson 1978, Harris 1979) and cormorants (Rasmussen 1989). Here, we argue that the Great Frigatebird acquires its full adult plumage through a single protracted post-juvenile moult (Prebasic I—Palmer 1972) rather than through several consecutive periodic moults as is usually thought. Therefore, the several plumages displayed by immature Great Frigatebirds are likely to be transitional stages of the post-juvenile moult rather than true intermediate plumages produced through periodic moults.

Why do frigatebirds protract plumage and sexual maturation?

The extensive period that the Great Frigatebird, and apparently other frigatebirds (Diamond 1975, Nelson 1976), require for plumage and sexual maturation remains enigmatic. For example, the biology of frigatebirds suggests that the proposed hypotheses for delayed plumage maturation may not apply to them. Frigatebirds remain largely free from predation at all age-stages. Immature male and female frigatebirds display similar body plumage that is distinctive from that of adult females, and birds wearing immature plumage rarely attempt to breed. Therefore, neither the cryptic nor the female mimicry hypotheses explain a delay in plumage maturation. Among frigatebirds, immature birds are subordinate to both males and females, and males (which are smaller than females) are subordinate to females (C.A. Valle unpubl. data, but see Gibbs & Gibbs 1987).

That a distinctive immature plumage reduces aggression by adults on foraging grounds is unlikely, because foraging juvenile and immature birds are frequently attacked by adults (Gibbs & Gibbs 1987, C.A. Valle unpubl. data). An immature plumage therefore does not play a generalized status-signalling role during the extended prebreeding period in frigatebirds. Furthermore, strictly speaking, frigatebirds do not have delayed plumage maturation (delayed acquisition of adult plumage by sexually mature birds—see Rohwer *et al.* 1980, Rohwer & Butcher 1988, Thompson 1991). Instead sexual and somatic (plumage) maturation are correlated, and birds wearing subadult plumages have not been found to breed.

However, frigatebirds, especially immature ones, face major difficulties in gathering enough food to meet their daily energy demands and so are adapted to long periods of fasting (Nelson 1976, Valle 1986). By extending the duration of the post-juvenile moult, frigatebirds may avoid the substantial increase in daily energy and nutrient demands. In support of a single extended post-juvenile moult of body plumage in the Great Frigatebird, and presumably in other frigatebirds, we have found that adult Great Frigatebirds are able to arrest moult and retain feathers, even flight feathers, for up to four years (Valle 1986), in spite of the negative impact that old ragged flight feathers may have on flight performance. The high energetic cost of moulting also is a likely explanation of why several marine birds, including frigatebirds, extend the flight feather moult over several months to more than a year (Kendeigh *et al.* 1977, King 1980, Walsberg 1983, King & Murphy 1985). This is also presumed to be the reason why several tropical seabirds arrest their moult to commence breeding (Ashmole 1971, De Korte & De Vries 1978).

Furthermore, because of their highly specialized feeding technique, frigatebirds may not be under strong selective pressure to moult body plumage every year. Frigatebirds feed on the wing (i.e. they do not enter the water when feeding—Nelson 1976, Valle 1986), and so the rate of body-plumage wear is expected to be slow. Moreover, they have no great need for body plumage insulation, unlike most seabirds (Ashmole 1971, Palmer 1972, Payne 1972, Diamond 1976, Furness 1988, Melville 1991). Therefore, frigatebirds may extend their body-plumage moult over several years with little impact on foraging ability, while reducing the energy demands and physiologic stress that moulting involves.

We propose that the adaptive significance of a slow extended period for plumage maturation in frigatebirds arises from the energy-saving benefits to subadult survival that result from extending post-juvenile moult over a long period. This is a form of the moult constraints hypothesis (see Rohwer *et al.* 1983, Rohwer 1986, Rohwer & Butcher 1988) in which distinctive subadult plumages in frigatebirds may not be adaptive *per se.* Marine ornithologists have widely recognized that slow plumage maturation in frigatebirds, as well as in several other marine birds, might result from the advantages of reduced daily energy demands on young birds (e.g. Nelson 1976, 1983; MacLean 1986; Burger 1987). The slow sexual maturation of frigatebirds might also be related to immature birds requiring a long period to learn and improve foraging skills (Nelson 1976, Valle 1986) and to their presumed great longevity (Valle 1986, Joula *et al.* in press). These arguments are also consistent with Studd & Robertson's (1985—but see Montgomerie & Lyon 1986) breeding-threshold hypothesis and with predictions from life-history models (e.g. Williams 1966, Lack 1968, Ricklefs 1977, Horn 1978, Wittenberger 1979, Horn & Rubenstein 1984) that delaying breeding or avoiding the energy cost of annual moult in a long-lived organism may be beneficial to an individual's lifetime reproductive success.

Is a distinctive juvenile plumage adaptive in frigatebirds?

The adaptive value of a distinctive white plumage in juvenile frigatebirds remains unclear. If having a white plumage has no advantage during the prebreeding subadult stage, then why do not frigatebird nestlings directly develop a black juvenile plumage similar to that of adults? Black feathers are stronger and more resistant to wearing from abrasion (Barrowclough & Sibley 1980, Bonser 1995), and relative to white feathers, melanin-based feather colouration may not be particularly expensive to produce (McGraw & Hill 2000, McGraw *et al.* 2002). An energy or nutrient constraint hypothesis may, therefore, not be a plausible explanation.

We have already argued that a distinctive white immature plumage might accrue no benefit during the subadult stage. However, a distinctive white immature plumage may serve as a status-signalling mechanism that reduces aggression from courting males while dependent juveniles remain at the nest site. Among frigatebirds, the breeding cycle lasts more than a year. Therefore, when the next breeding season starts, fledged juveniles from the previous year are still dependent on their parents for food and remain largely attached to their nest site, where they usually return to be fed (Nelson 1976, Valle 1986). Thus, courting males sit side-by-side with juveniles from previous years in the courting grounds. In agreement with our hypothesis, our observations showed that males in courtship, and those recently mated, which usually are more aggressive, were highly tolerant toward juveniles and only rarely attacked them when at their nest site.

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