# PARENTAL CARE IN FRIGATEBIRDS: A COMPARISON BETWEEN TWO SYMPATRIC SPECIES

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# RÉSUMÉ

La participation des deux sexes aux soins parentaux a été étudiée chez deux espèces de frégates: la Frégate du Pacifique (Fregata minor), présentant un dimorphisme sexuel de taille marqué, et la Frégate ariel (Fregata ariel), présentant un dimorphisme sexuel de taille plus faible. Nos résultats montrent que, chez la Frégate du Pacifique, une participation différentielle des deux sexes aux soins parentaux existe: les mâles désertent le nid trois mois environ après l'éclosion et les femelles prennent en charge, seules, la longue phase d'élevage restante. Au contraire, chez la Frégate ariel, mâles et femelles semblent participer de façon équitable à l'élevage du petit au moins jusqu'à son envol. Ces résultats sont discutés dans le contexte des hypothèses explicatives du dimorphisme sexuel inversé de taille.

#### SUMMARY

The participation of both sexes to parental care have been studied in two different frigatebird species: the Great Frigatebird (Fregata minor), exhibiting a clear sexual size dimorphism, and the Lesser Frigatebird (Fregata ariel), with little sexual size dimorphism. Our results show that Great Frigatebirds perform an unequal division of labour during the chick rearing period: males desert the nest around three months after hatching and females undertake alone the long remaining chick rearing period. On the other hand, male and female Lesser Frigatebirds share equally parental duties until the chick is able to fly. These results are discussed in the light of explicative hypotheses of Reversed Sexual Size Dimorphism.

#### INTRODUCTION

Sexual dimorphism in adult body size is classically explained as a product of different natural selective pressures (Darwin, 1871) which act differentially

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between males and females. These selective pressures are generally separated into two categories: ecological versus reproductive (Anderson, 1994; Bonnet et al., 1998, 2001). The evolution of traits that maximize organism survival is classically linked to ecological selection (Arnold & Wade, 1984a, b) whereas the evolution of traits that maximise current reproductive success is linked to reproductive selection (Anderson, 1994). Reproductive selection is involved when adaptive traits optimize mating success (intra- or inter-sexual selection) or directly reproductive output (fecundity selection; Anderson, 1994). Sexual dimorphism results from the combination of different kinds of synergetic or antagonistic selective pressures (ecological and reproductive), which can affect together the evolution of male and female adult body size (Newton, 1979; Berry & Shine, 1980; Shine, 1989; Mueller, 1990). The evolutionary scenario explaining the sexual size dimorphism (SSD) in some species is often difficult to reconstitute because of the impossibility to tease apart these different selective pressures. For example, an adaptation maximizing males' access to trophic resources can also enhance males' access to females, because of a better body condition (Grant & Grant, 1987). Indeed, sexual dimorphism remains a puzzling problem in evolutionary biology.

Before understanding the evolutionary causes and consequences of sexual size dimorphism, it is necessary to clearly identify which sexual divergences in biology and ecology are associated with sexual size dimorphism. The aim of this study is to highlight such biological SSD correlates, in a bird family where species have very contrasted intensity of sexual size dimorphism: the frigatebirds. We focused here our attention on the respective participation of males and females to parental care in two species of frigatebirds: the highly dimorphic Great Frigatebird (Fregata minor), and the Lesser Frigatebird (Fregata ariel), with little sexual size dimorphism. In both species, females are larger than males'. Two hypotheses will be investigated here: (1) dimorphic frigatebird species exhibit a sex biased division of parental labour and (2) the more dimorphic the species, the more the sexual bias is strengthened.

## **METHODS**

The study has been conducted at Europa Island (22°20'S, 40°22'E), in the Western Indian Ocean, Mozambique channel. Data were collected between 24 February and 25 April 1997. Approximately 1,700 to 2,300 pairs of Great and Lesser Frigatebirds breed on the island (Le Corre & Jouventin, 1997), separated in two main colonies. In the "Baie des Congres" colony, both species breed together, whereas in the "Grand Gùrù" colony, only Great Frigatebird breeds. Frigatebirds nest in arborescent Euphorbia (Euphorbia stenoclada), nests being distributed between 1 and 6 meters high. Great Frigatebird nests in scattered groups of no more than ten nests whereas Lesser Frigatebird nests in dense groups of up to 100 pairs. Both species are timorous, and often leave the nest when an observer approaches. Any nest with an egg or a new born chick left unguarded for a few minutes is immediately sacked by other congeners searching for twigs to build their own nest, which inevitably leads to the fall of the egg and thus breeding failure (pers. obs.).

Adults Great Frigatebird were captured at night with a landing net, while roosting outside of the breeding colony. We measured bill length and depth with callipers ( $\pm$  0.1 mm). The wing and outer tail-feather lengths were measured with a steel rule ( $\pm$  0.5 mm). Birds were weighed with a Pesola ( $\pm$  10 g). Because Lesser Frigatebird roosts inside or close to the colony, we could not catch them. Then biometric data from this species were derived from literature (Marchant & Higgins, 1990). The body size dimorphism index (D.I.) was calculated following this formula: D.I. =  $Mm/Mf \times 100$  (with Mm: male measurement; Mf: female measurement).

# CHICK AGE

Because growing curves were not available for these two frigatebird species in this locality, and can markedly differ between populations or between years, we broadly estimated the age of chicks in the study colony, based on Diamond's plumage development criterions (Table I; Diamond, 1973).

Table I

Correspondence between chick stages, plumage development, and estimated chick age. Data are drawn from Diamond, 1973

Chick stages	Description	Estimated age Incubation period: 40 to 55 days		
1	Egg			
2	Downy chick, with growing scapular feathers	3 weeks old		
3	Wing covert feathers present	6 weeks old		
4	Growing primaries and tail feathers	9 weeks old		
5	Scattered down on neck and belly	14 weeks old		
6	Fully feathered	18 weeks old		
7	Fully feathered and flying chick	24 to 44-72 weeks (afterwards chick becomes independent)		

# MALE AND FEMALE PARTICIPATION TO PARENTAL CARE

# Incubation

We measured male and female participation to incubation duties by making 300 to 400 meters long transects through both the breeding colonies, the first of

March 1997, the 14 and the 15 of April 1997. We made 2 transects for Great Frigatebird and 2 for Lesser Frigatebird. During the transects, we counted the proportion of males and females incubating (n incubating =108 for Lesser and 133 for Great Frigatebird).

# Chick rearing period

Because night feeding visits seem scarce on Europa island (pers. obs. and Lagarde *et al.*, 2001), we studied male and female participation to chick feeding only during day hours. Observations were made from a hiding place with  $10 \times 42$  binoculars.

We performed eight focal sessions on Lesser Frigatebird, in the period 03-27.III.97, totalling 38.5 hours of observation, equally divided between AM (7 h 30 to  $12\ h$  00) and PM ( $12\ h$  00 to  $19\ h$  00). The high sensibility of this species to human disturbance prevented us to manipulate birds and to make close observation of breeding colony. Consequently, the hiding place was settled at about 100 m from the nests. Because we could not mark the birds or the nests individually, we did not measure individual performance but instead the whole proportion of male and female feeding visits for every chick stage in the breeding colony.

We observed Great Frigatebird nests continuously from 7 h 30 to 19 h 00 during 6 consecutive days, from the 2.IV.97 to the 7.IV.97, totalling 69 hours of observation. Because Great Frigatebird is less sensitive to disturbance than Lesser Frigatebird, the hiding place was settled at about 30 m from the nests and we could closely observe 50 nests individually. We then measured the diurnal feeding frequency performed by each parent, and for each chick stage respectively. However, in order to compare both species, we also calculated, as in Lesser Frigatebird, the whole proportion of male and female feeding visits for every chick stage in the breeding colony. The total number of feeding visits observed was 156 for *Fregata ariel* and 202 for *Fregata minor*.

#### STATISTICAL ANALYSES

Sexual differences in biometrical measures and Great Frigatebird feeding frequency (log transformed) were tested using a one-way ANOVA with sex as factor. To test the sexual divergence in the feeding frequency, we used a two-way ANOVA, with sex and chick stage as factors, followed by LSD post-hoc comparisons. In both species, we tested differences between proportion of males and females seen incubating an egg or feeding their chick by using  $x^2$  square tests, for each chick stage separately. Such methodology did not preclude individual bias in our results, because of possible repeated observations on the same birds. Nevertheless, the large sample size per chick stage should minimize such bias. All statistical tests were performed using Statistica 5.1 (Statsoft, 1997). All data are presented as means  $\pm$  standard error.

#### SEXUAL SIZE DIMORPHISM

Females Great Frigatebird are significantly larger than males for all measurements carried out (Table II.1). The highest dimorphism indices were found in, respectively, body weight (I.D. = 85%), culmen length and bill height (I.D. = 88%). Sexual dimorphism was much less pronounced in Lesser Frigatebird, males and females differing significantly only in culmen length which was larger in the female (I.D. = 91%, Table II.2).

TABLE II.1

Body measurements of adults Great Frigatebird breeding on Europa Island.

Data are Mean ± Standard variation, values in brackets are sample sizes

	Body mass (g)	Wing chord (mm)	Tail (mm)	Culmen length (mm)	Culmen width (mm)	Culmen depth (mm)
Males	1114 ± 100 (32)	576.7 ± 30.3 (32)	$400.5 \pm 3.8$ (32)	98.1 ± 0.3 (32)	$26.7 \pm 0.1$ (32)	$15.0 \pm 0.1$ (31)
Females	$1304 \pm 95$ (31)	601.8 ± 33.5 (31)	$424.3 \pm 0.3$ (31)	$111.2 \pm 0.3$ (31)	$28.4 \pm 0.1$ (30)	$17.0 \pm 0.2$ (30)
F	59.27	12.83	6.00	184.14	30.56	25.21
P	< 0.001	< 0.001	0.012	< 0.001	< 0.001	< 0.001
ID%	85.4	95.82	94	88	94	88

Body measurements of adults Lesser Frigatebird.

Data are obtained from literature: (a) Nelson, 1975, (b) Marchant & Higgins, 1990

TABLE II.2

	Body mass (g)	Wing chord (mm)	Tail (mm)	Culmen length (mm)	Culmen width (mm)	Culmen depth (mm)
Males		533.5 ± 13.7 (4)	316.5 ± 9.8 (4)	82.2 ± 2.7 (4)	ing a series of the series of	
Females	- ·	$547.0 \pm 9.3$ (5)	$318.4 \pm 3.3$ (5)	$89.4 \pm 2.5$ (5)		
F	-	3.11	0.16	1,720	1 20	
, P	-	0.1	> 0.05	< 0.001		
ID%	94 (a)	97.5 (b)	99.4 (b)	91.9 (b)		- 1 <u>-</u> 1

No significant difference appeared in Lesser Frigatebird with regard to the proportion of males and females incubating or rearing a chick, although the number of males observed in the late chick stages (6 and 7) tended to decrease (Fig. 1).

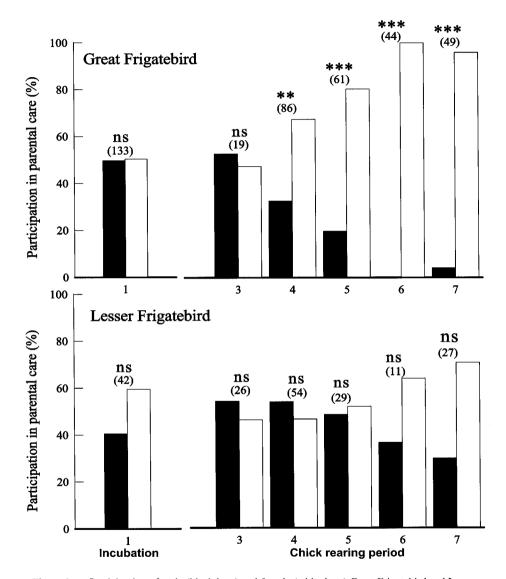


Figure 1. — Participation of male (black bars) and female (white bars) Great Frigatebird and Lesser Frigatebird to parental care during the incubation and chick rearing periods. The sample size (number of adults observed per chick stage) is in brackets at the top of the bar. Asterisks refer to differences between males and females. \*\*\*: < 0.001, \*\*: < 0.01.

In Great Frigatebird, no significant difference appeared in the proportion of males and females incubating or rearing a chick until stage 4. From this stage onward, the number of males observed feeding the chick was significantly lower than the number of females (Fig. 1). From stages 6 and 7, males were never seen again.

Great Frigatebird feeding frequency was significantly affected by chick stage  $(F_{4,90}=3.56,P=0.009)$ , and sex  $(F_{1,90}=16.14,P<0.001)$ , but there was no effect from the interaction between chick stage and sex of adult  $(F_{4,90}=4.93,P=0.20)$ . From chick stage 4 onward, feeding frequency was higher in females (post-hoc tests: chick stage 3: P=0.66, 4: P=0.0046, 5: P<0.001, 6: P<0.001, 7: P=0.006; Fig. 2).

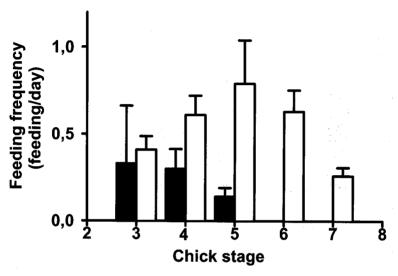


Figure 2. — Variation of male (black bars) and female (white bars) feeding frequency throughout chick stages in Great Frigatebird. Values are means ± standard deviation.

#### DISCUSSION

Our results clearly show that, in the highly dimorphic Great Frigatebird, males desert rapidly the nest and females assume alone most of the long chick rearing period. Such sexual division of parental care has been already observed in Great Frigatebird from Aldabra (Diamond, 1973) but our results allow to precise the timing of desertion in males. Two months and a half after egg-laying, in one third of the nests males were never observed to feed the chick during our six-day continuous observation and were therefore considered to have deserted the nest. Four months and a half after egg-laying, the great majority of females were rearing the chick alone. This implies that females performed alone the remaining rearing period, plus the long post-fledging care period. In the more dimorphic Magnificent Frigatebird, F. magnificens (D.I. body mass = 75%, Cramps & Simmons, 1977),

breeding adults have a stronger unequal division of labour during the chick rearing period: males deserted the nest when the chick was approximately 2-3 months old (Diamond, 1972; Osorno, 1999) but the timing of desertion varied greatly between males (from 18 to 161 days after hatching), depending they were early or late breeders (Osorno, 1999). In our study, the high interindividual variation in feeding frequency in the early chick stages also suggests that the timing of males nest desertion varies strongly between individuals too. Great Frigatebird is found breeding all the year round on Europa, but many pairs start breeding at the end of the winter (Le Corre, 2001). Thus, there could be, as in Magnificent Frigatebird, early and late breeding pairs, and some males might therefore desert the nest much earlier than others.

On another hand, our results show that males and females of the much less dimorphic Lesser Frigatebird shared more equally parental duties than those of the Great Frigatebird, as also shown in the population of Aldabra (Diamond, 1973). However in our study, there was a trend for males Lesser Frigatebird to decrease their participation in the late rearing period. We might have underestimated such a male disengagement due to the long duration of chick stage 7: this stage includes the post-fledging period, when the flying chick is still fed by adults, and can last from 5 months to 1 year! (Diamond, 1973). We cannot therefore definitively exclude the possibility that males Lesser Frigatebird desert the nest during the post-fledging care period. Unfortunately, the use of plumage criterion to give a rough estimation of chick age prevented us to obtain a more precise time schedule of nest desertion by males. Indeed, such a description would require individual observation over a long period with chick of known age.

Male and female participation to parental duties differs in many dimorphic species and the "sexual division of labour" hypothesis suggests that sexual size dimorphism may be a consequence of different roles devoted to males and females throughout breeding (Newton, 1979; Andersson & Norbeg, 1981; Lunberg, 1986; but see Guerra & Drumond, 1995). According to this hypothesis, natural selection acts differentially on male and female body size because of the specific task they perform (Guerra & Drummond, 1995). Accordingly, in frigatebird species, the intensity of RSSD seems well paralleled by the intensity of sexual divergences in the participation to parental care.

As suggested in our study and in others (Diamond, 1973; Osorno, 1999), it is likely that in Great Frigatebird and other dimorphic frigatebird species, the early nest desertion performed by small males during the chick rearing period could allow them to breed annually. Contrarily, larger females are able to bring more food to the chick (Osorno, 1996; Lagarde et al., in prep.) and alternatively to cope with the prolonged parental effort which is required until the definitive emancipation of the young. In turn, females presumably exhausted by their extremely long rearing period might take a "sabbatical" before starting a new breeding attempt (Nelson, 1975). To date we still do not dispose from any individual survey to confirm this hypothesis in the Great Frigatebird. However such a view may be supported by observations made by Diamond (1973) on Aldabra who reported that sex-ratio was male-biased in groups of displaying Great Frigatebirds.

The strong sexual division of parental care observed in the most dimorphic frigatebirds may be associated with sexual differences in the strategies optimizing breeding success. Individuals are expected to optimize their reproductive investment to produce the maximum number of offspring over their lifetime (Trivers, 1972). However male and female Great Frigatebird differ in the compromise they

do in the trade-off between current and future reproduction: males participate little to the rearing of the chick but rather favour a high number of mating opportunities, while females invest more in the quality of the offspring they produce (Emlen & Oring, 1977; Nelson, 1983; Osorno, 1999).

On another hand, in the less dimorphic Lesser Frigatebird, the equal sharing of parental duties between mates could allow adults to breed only every two years (Orta, 1992). This is also supported by the equal sex-ratio observed in displaying group of Lesser Frigatebirds on Aldabra (Diamond, 1973).

Then, why frigatebirds do not exhibit the same sex division of labour and, hence, the same divergent breeding strategy? We must not exclude the possible, and probable, influence of other factors such as divergences in foraging ecology. It has been suggested for birds that a partition of foraging niches between sexes should arise in tropical areas where food availability is limited, or follows unpredictable variations, in order to optimize the foraging profitability of both males and females (Selander, 1972; Fairbairn & Shine, 1995). Then other selective pressures may shape the SSD of tropical birds. In boobies, despite females are larger than males, the division of labour is rather weak and does not seem to explain the observed RSSD (Guerra & Drumond, 1995), but sexes may differ in their foraging range (Gilardi, 1992). At Europa Island, Great Frigatebird exhibits a strong sexual divergence in feeding ecology whereas Lesser Frigatebird seems to concentrate foraging efforts in pelagic waters (Lagarde et al., 2001 and in prep.). Then, to identify and pool apart the different selective pressures acting on frigate bird SSD and to identify causal relationship between RSSD and ecological correlates, it is necessary to investigate other aspects of frigatebird ecology such as feeding ecology and foraging strategies.

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