

GREAT FRIGATEBIRD SIZE DIMORPHISM ON TWO CENTRAL PACIFIC ATOLLS¹

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Abstract. We examine sexual size dimorphism in Great Frigatebirds (*Fregata minor*) on Johnston Atoll and Christmas Island, Central Pacific Ocean, using univariate and multivariate analyses. Adults are larger on Johnston than on Christmas in the four variables measured (culmen, wing, tail, and mass), but greater dimorphism between the sexes exists on Christmas. We relate these morphological data to environmental variability and predictability and the various published hypotheses on the evolution of sexual size dimorphism.

Key words: Great Frigatebird; sexual dimorphism; multivariate analysis; Christmas Island; Johnston Atoll.

INTRODUCTION

Sexual size dimorphism interests all of us, and the phenomenon has received considerable attention in birds, particularly because the larger sex differs between groups (review by Jehl and Murray 1986). The causes and consequences of dimorphism from an ecological view remain open to question (Power 1980, Payne 1984, Jehl and Murray 1986), and the degree of dimorphism is of concern to taxonomists who desire to know the size limits of species (Olson 1977).

Our studies of ecology and breeding biology of the seabirds nesting on Christmas Island (2°N, 157°W) and Johnston Atoll (16°N, 169°W) in the Pacific Ocean allow us to examine sexual size dimorphism in Great Frigatebirds (*Fregata minor palmerstoni*). We used univariate and multivariate statistics to determine the degree of the size variation between age classes, sexes, and geographically discrete populations. Juveniles and fledglings were included in this analysis because there appeared to be a difference in the timing of the onset of sexual dimorphism exhibited by frigatebirds on the two atolls.

During 1982 to 1983 a major oceanographic climatological event, the El Niño-Southern Oscillation (ENSO) occurred (Barber and Chavez 1983), resulting in a more than 75% decline in the breeding population of most seabirds on Christmas Island. There are no data for Johnston during this time, although counts of birds from previous years and our counts for 1983 to 1987,

indicate that no noticeable loss of adults occurred (Schreiber and Schreiber 1984). A minor ENSO occurred in 1986 to 1987 (Climate Diagnostics Bulletins 1986-1987), affecting adult weights and nestling growth rates on both Christmas and Johnston (Schreiber and Schreiber, unpubl. data). Mayr (1963) suggested that a temporary bottleneck in population size can perturb a population morphologically from equilibrium. The 1982-1983 ENSO provided us with a unique opportunity to investigate the impact of a severe ecological perturbation and resultant decline in population size on Christmas. These data may yield some insight into the types of selective pressures important in favoring such diverse traits as sex ratios, population structure, and morphology.

METHODS

We captured roosting and nesting birds. Birds were banded, the culmen, wing, and tail length were measured with a meter stick, and mass was determined by placing birds in a pillowcase attached to a tared 2,000-g Pesola scale. We recorded sex and age (adult, fledgling, juvenile) of each bird based on plumage characteristics (Harrison 1983; Schreiber and Schreiber, unpubl. data).

We measured birds on Christmas Island in March and August 1979, July 1980, July 1982, February, July, and October 1983 to 1985, February and July 1986, and on Johnston Atoll in June 1983, and February, July, and October 1984 to 1985, February and July 1986, February 1987.

We performed all statistical analyses on the IBM 3081 computer at the University of Southern California, using the Statistical Analysis Sys-

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tem (SAS). Univariate analyses include correlation, regression, and analysis of variance, including appropriate adjustments for unequal sample sizes.

Multivariate analyses performed were a discriminant function to predict sex, and canonical variates analysis. The discriminant function was determined from half the individuals on each island and the classification criterion was applied to the other half of the individuals. Pooled covariance matrices were used. We used canonical variates analysis (a discriminate function) to summarize differences between sexes and ages on both islands as they relate to the total variation in all adults. Canonical variates analysis is a data reduction technique, which can be used for statistical tests as well as for exploration. It provides a linear combination of the four variables (culmen, wing and tail length, and mass) that has the highest possible multiple correlation with the chosen groups and can be used to assess differences among groups, such as sex or age. The squared Euclidean distances between the centroids in the canonical variates space are reported as Mahalanobis generalized distances which indicate the relative distance between the groups specified. Sample sizes are weighted and variables are standardized to account for differences in measures used.

We performed three separate canonical variates analyses on these data to test for the effects of the following groups: (1) how sexes differ between islands; (2) how adults, juveniles, and fledglings differ on each separate island; and (3) how sexes differ on each separate island.

These multivariate analyses allow us to consider a combined set of morphological variables on each individual within a population and thus to look for biologically meaningful patterns of covariation among the variables. Covariation (or lack thereof) can be determined with these analyses even if there is no obvious relationship in the original data.

RESULTS

UNIVARIATE ANALYSES

Means, standard deviations, ranges, and sample sizes for each age and sex class are presented in Table 1. Great Frigatebird adults are larger on Johnston than those on Christmas; females are larger than males on each island; ratios between females and males are greater on Christmas. Mass

is the most dimorphic character on both islands, followed by culmen. Two-way ANOVAs for each measurement for the effect of sex on each island are all significant on Christmas ($P < 0.0001$), and only significant for culmen and mass on Johnston ($P < 0.0001$). These data indicate that the sexes are more dimorphic on Christmas.

Juveniles undergo a much greater loss of mass on Christmas than on Johnston before obtaining adult plumage (Table 1). This may be an artifact of sample size for Johnston, where juveniles roost in inaccessible sites and thus are rarely caught, but we believe it also reflects greater difficulty in finding food on Christmas.

An analysis of variance of each measurement by island for the effect of year *and* season showed no significant differences in culmen, wing, or tail length on either island. Testing for the effect of season only, adults were heaviest on Johnston in October (Table 2, females $P < 0.002$, males $P < 0.01$) when most birds caught are on eggs. In June to July adults were lightest ($P < 0.002$ females) when the majority are feeding chicks, although 25% of those caught were on eggs. Seasonal variation on Christmas was not significant. Most eggs are laid in February but some eggs are present throughout the year. Mass of adults on both islands was generally lowest in 1982 (data for Christmas only) and 1986, with some variation between sexes, illustrating the effects of the ENSOs which occurred in those years (Table 2).

MULTIVARIATE ANALYSES: DISCRIMINATE FUNCTION ANALYSIS

A discriminate function, based on the pooled covariance matrix, determined using the four measurements from each individual adult, enabled us to sex 98% of individuals correctly on Christmas, and 90% on Johnston. The greater accuracy on Christmas is due to the greater separation between the sexes in size on that island.

MULTIVARIATE ANALYSES: CANONICAL VARIATES ANALYSIS

Effect of both sexes and both islands, adults only. This analysis describes the differences between males and females on the two islands and between the islands. Separation on the first axis is due primarily to culmen length and accounts for almost all (91.5%) of the separation between these groups (Fig. 1, Table 3, loading on Axis 1 Standardized Canonical Coefficients = 2.078). Johnston males and Christmas females have similar

TABLE 1. Great Frigatebird means of measurements, female to male ratio, and analysis of variance results for sex by island.

	Culmen (mm)	Wing (mm)	Tail (mm)	Mass (g)
Johnston Atoll				
Fledglings	106.49 ± 8.57 ¹ 92–123 ² (67) ³	522 ± 70.72 370–600 (55)	287 ± 94.30 120–405 (51)	1,305 ± 179.35 780–1,690 (62)
Juveniles	110.76 ± 7.73 100–126 (21)	560 ± 38.94 442–606 (21)	356 ± 24.34 325–395 (9)	1,222 ± 150.00 1,000–1,525 (16)
Males	102.36 ± 3.09 95–108 (49)	533 ± 35.75 407–592 (33)	375 ± 10.52 355–390 (20)	1,234 ± 102.09 975–1,450 (51)
Females	113.86 ± 5.07 102–124 (21)	560 ± 19.70 530–585 (27)	376 ± 26.27 320–410 (12)	1,478 ± 129.18 1,210–1,700 (23)
Female/male	1.11	1.04	1.00	1.18
ANOVA: sex ⁴	<i>P</i> < 0.0001	ns	ns	<i>P</i> < 0.0001
Christmas Island				
Fledglings	98.87 ± 7.44 84–115 (81)	538 ± 82.58 430–600 (73)	350 ± 33.95 270–410 (61)	1,083 ± 182.66 650–1,475 (78)
Juveniles	100.26 ± 7.51 84–120 (159)	572 ± 22.31 500–620 (54)	366 ± 48.18 227–440 (43)	942 ± 202.17 550–1,430 (169)
Males	92.20 ± 3.33 83–108 (270)	552 ± 18.31 460–590 (80)	398 ± 20.79 320–445 (52)	927 ± 110.87 640–1,350 (316)
Females	106.34 ± 4.11 94–116 (279)	570 ± 26.97 460–608 (91)	418 ± 29.67 285–495 (71)	1,183 ± 115.47 850–1,550 (312)
Female/male	1.15	1.04	1.05	1.28
ANOVA: sex	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001

¹ Standard deviation.² Range.³ Sample size.⁴ This analysis of variance indicates the probability that the differences between sexes on each island are significant.

culmen lengths and do not separate on this axis. The two populations of females are closer in size to each other than are the males.

The second axis, which separates the two is-

lands to some extent, has the highest loading for tail and smaller loadings for wing and mass, mass being negative. Johnston birds thus fall below Christmas birds on this axis because they have

TABLE 2. Comparison of monthly (seasonal) and annual mass (g) for adult Great Frigatebirds on Johnston Atoll and Christmas Island.

Months	Johnston		Christmas	
	Females	Males	Females	Males
October	1,585 (7) a ¹	1,298 (20) a	1,237 (7) a	950 (4) a
February	1,450 (14) b	1,194 (21) b	1,211 (69) a	967 (85) a
July	1,300 (2) c	1,192 (10) b	1,175 (256) a	913 (243) a
<i>P</i> <	0.002	0.01	ns	ns
Year				
1967			1,208 (18) ab	960 (17) ab
1979			1,192 (42) ab	940 (67) ab
1980			1,199 (56) ab	939 (52) ab
1982			1,141 (110) b	881 (111) b
1983			1,206 (10) ab	993 (10) a
1984	1,550 (6) a	1,292 (20) a	1,269 (34) a	986 (19) a
1985	1,465 (6) a	1,228 (13) ab	1,189 (33) ab	953 (36) ab
1986	1,367 (6) b	1,094 (7) b	1,159 (24) b	942 (20) ab
1987	1,540 (5) a	1,239 (10) ab		
<i>P</i> <	0.003	0.0001	0.0001	0.0001

¹ Numbers not sharing a letter are significantly different from each other (comparisons to be made within columns).

greater mass and proportionately shorter tails and wings than do Christmas birds.

All Mahalanobis generalized distances between centroids are highly significantly different (Table 3). This indicates that all four groups are significantly different from each other. The largest distance is between Christmas males and Johnston females (7.385). The distance between sexes is greater on Christmas (4.335) than on Johnston (3.744). Thus, sexual dimorphism on the two islands is not just a function of scaling, because the larger Johnston birds are less sexually dimorphic.

Effect of sex, on each island separately, adults only. The results of this analysis are slightly different between islands (Table 3). On Johnston, culmen length separates the sexes on the first axis ($P < 0.0001$) with some contribution of mass, and a smaller contribution of tail (negative). So that while culmen and mass increase, tail length does not increase proportionately. On Christmas, culmen length is a stronger separator of the sexes, having a higher loading on the first axis ($P < 0.0001$), and a lesser contribution of mass. There are no negative loadings. This illustrates that shape as well as size differences exist between the populations on the two islands. The ratio of female to male mass is greater than the ratio of female to male culmen length (Table 1),

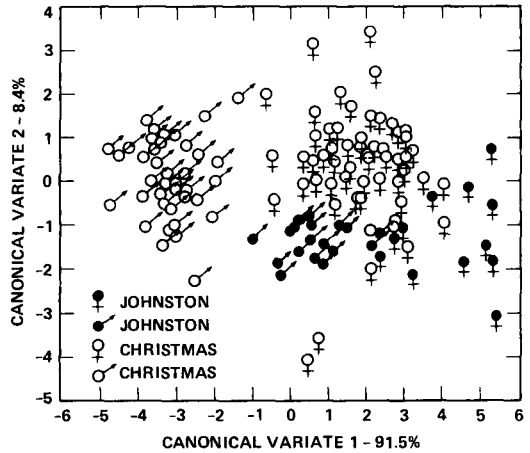


FIGURE 1. Plot canonical variates axes 1 and 2 for the effect of island and sex (adults only). Data from Table 3.

but culmen length is shown here to be a more definitive separator of the sexes.

The greater values in the Christmas results plus the greater Mahalanobis distance on Christmas indicate a greater separation between the sexes there although the distances between the sexes on each island are highly significant.

Effect of sex and age (males, females, juveniles, and fledglings) for each island separately. This

TABLE 3. Results of canonical variates analyses for the effect of island and sex (adult birds only), and for the effect of sex, by island, with Mahalanobis generalized distances between groups.

	Island and sex		Sex: Johnston Atoll	Sex: Christmas Island			
	Axis ¹	Axis ²	Axis ¹	Axis ¹			
Canonical correlation	0.918 ¹	0.575 ¹	0.853 ¹	0.913 ¹			
Eigenvalue	5.358	0.494	2.724	4.992			
Percent of variation accounted for by each axis	91.5%	8.4%					
Standardized canonical coefficients							
Culmen	2.078	0.268	1.442	2.083			
Wing	0.059	0.443	0.039	0.126			
Tail	0.080	0.913	-0.259	0.052			
Mass	0.526	-0.508	0.684	0.399			
Mahalanobis generalized distances between classes ²							
	Island and sex			Sex: Johnston	Sex: Christmas		
	Christmas ♀	Johnston ♂	Johnston ♀	Johnston ♂	Christmas ♂		
Christmas ♂	4.335	3.777	7.385	Johnston ♀	3.277	Christmas ♀	4.490
Christmas ♀		2.067	3.523				
Johnston ♂			3.744				

¹ $P < 0.0001$.

² All Mahalanobis distances are highly significant ($P < 0.0001$).

TABLE 4. Results of canonical variates analyses for the effect of age and sex by island (includes adults, juveniles, and fledglings), and Mahalanobis distances between groups.

	Johnston Atoll			Christmas Island		
	Axis ¹	Axis ²	Axis ³	Axis ¹	Axis ²	Axis ³
Canonical correlation	0.6361 ¹	0.4779 ¹	0.2860 ²	0.7025 ¹	0.6310 ¹	0.4193 ¹
Eigenvalue	0.6798	0.2961	0.0891	0.9743	0.6616	0.2133
Percent of variation accounted for by each axis	64.0%	27.8%	8.4%	52.6%	35.7%	11.5%
Standardized canonical coefficients						
Culmen	-0.4097	1.1388	0.8674	0.9239	-1.0037	0.1495
Wing	-0.9630	-0.4913	-0.1262	-0.1344	-0.1766	0.8952
Tail	2.2271	0.0708	-0.0234	0.7468	1.1418	-0.0107
Mass	0.8282	0.2527	-1.0792	0.2587	0.2603	-0.7827
Mahalanobis generalized distances between classes						
	Fledgling	Juvenile	Male	Female		
Fledgling		Christmas 1.377 ⁴	2.233	2.334		
Juvenile	1.086 ^{ns}		2.145	2.207		
Male	1.861 ³	1.749 ¹		2.613		
Female	2.131 ²	2.004 ¹	1.875 ¹			
		Johnston				

¹ $P < 0.0001$.² $P < 0.05$.³ $P < 0.01$.⁴ All Mahalanobis distances are highly significant on Christmas ($P < 0.0001$).

analysis examines the differences between the four groups on each island as they relate to the total variation for all individuals on the island. On both islands all three canonical axes are statistically significant (Table 4), though more so on Christmas, consistent with the larger Mahalanobis distances between the sexes of Christmas adults (Table 3).

On Johnston, tail length provides the most separation in the groups (64%, Axis 1) with smaller loadings for mass and wing (negative). This axis separates fledglings and juveniles from adults (Fig. 2). Wings of fledglings and juveniles are closer to fully grown than are tails, so that as tail length increases to adult size, wing length does not increase as much. The second axis separation is due to culmen length, again with a small negative loading for wing length, and separates the sexes. The negative loading for wing length illustrates that while females have longer culmens than males, wing length is not proportionately longer.

Culmen length separates the sex and age groups on Christmas, with smaller loadings for tail length (Table 4, Fig. 3). The sexes clearly separate on the first axis, which they did not on Johnston. The first axis accounts for 52.6% of the separa-

tion between the age groups. Fledglings and juveniles divide into two groups but it takes an interaction of both axes to separate them in to what must be males and females. Separation on the second axis (35.7% of the separation) is due to culmen (negative) and tail (positive), so that as the tail gets longer the culmen does not increase proportionately. Fledglings and juveniles have shorter tails and longer culmens proportionately than adults. The sexes are not as separate on this axis. Males fall higher on the axis, illustrating that they have longer tails proportionate to culmen length than do females.

The differences between the two islands in patterns of sexual dimorphism and age specific differences show that fledglings and juveniles are more sexually dimorphic (falling into two groups) following the same pattern as adults on Christmas. Johnston juveniles and fledglings are not clearly differentiated yet into sex. This may indicate an earlier onset of dimorphism on Christmas.

The Mahalanobis generalized distances between males, females, juveniles, and fledglings (Table 4) are all much larger, and more significant, on Christmas than Johnston, which is a function of the more significant separation be-

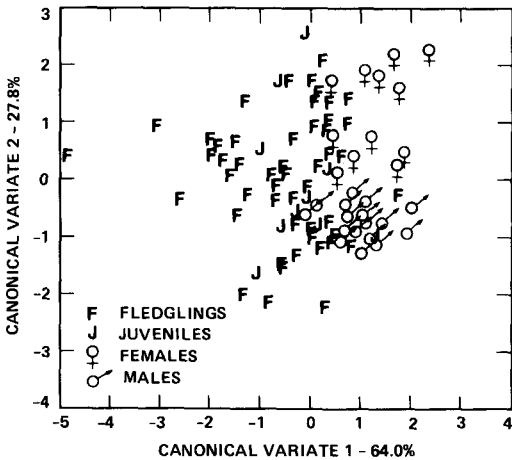


FIGURE 2. Plot of canonical variates axes 1 and 2 for the effect of age and sex on Johnston. Data from Table 4.

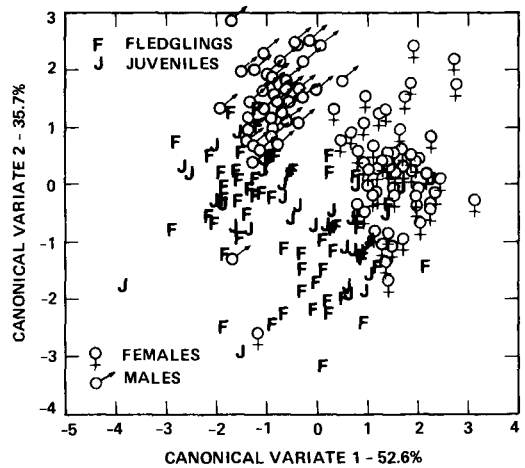


FIGURE 3. Plot of canonical variates axes 1 and 2 for the effect of age and sex on Christmas. Data from Table 4.

tween sexes. On both islands, the shortest distance is between fledglings and juveniles.

Canonical variates analyses of (1) males on both islands, and (2) females on both islands, show that males are more distant from each other than are females. This is illustrated in Figure 1, where females overlap between islands and males do not.

DISCUSSION

The greater degree of sexual size dimorphism in Great Frigatebirds on Christmas than on Johnston is intriguing. Because birds are larger in all age classes on Johnston it might be expected that dimorphism between sexes would be greater due to scaling. Both populations are presently classified as the same subspecies (*Fregata minor palmerstoni*, Mayr and Cottrell 1979), but few morphological data exist from throughout their range for comparison. We found that univariate statistics did not elucidate the differing patterns of variation in shape and size in this species as fully as do canonical variates analyses. Univariate statistics are presented as a documentation of morphologic variation and for comparison with other populations.

The lack of significant seasonal variation in mass on Christmas is probably the result of less seasonality in nesting there, given the lack of daylength and temperature controls on the equator (Schreiber and Ashmole 1970). Annual variation in mass on both islands reflects the effect of ENSO which is discussed later. Wing length

has generally been considered the most valid indicator of intraspecific body size in birds (James 1970, and references therein). However, in frigatebirds, we found wing length, along with tail length, to be the least dimorphic characters in adults between islands (Table 1). Culmen and mass are better indicators of body size.

GEOGRAPHIC VARIATION IN *FREGATA*

Fregata appears to have a similar pattern of dimorphism throughout its range. The ratios of female to male culmen length of Great Frigatebirds on the Galápagos, Christmas Island (Indian Ocean), Aldabra, in the Coral Sea (calculated from Nelson 1976), and Phoenix Islands (our measurements of museum specimens) all fall between our ratios for Christmas Island (Pacific Ocean, 1.15) and Johnson Atoll (1.11, Table 1). Wing, tail, and mass ratios are comparable among the islands. Mass on the Galápagos and Phoenix islands is the most dimorphic (1.32 and 1.37 respectively) of all localities, but is similar to Christmas (Pacific Ocean, 1.28). These three localities are in the equatorial Pacific. Few morphological measurements of other *Fregatidae* are available and a useful comparison throughout the range is presently impossible.

HYPOTHESES TO EXPLAIN THE ORIGIN AND FUNCTION OF SEXUAL SIZE DIMORPHISM

Many hypotheses regarding the origin and maintenance of sexual size dimorphism have been

proposed and discussed (see Ralls 1976, Mueller and Meyer 1985, Jehl and Murray 1986): sexual selection (Darwin 1871); females are greater size to produce an egg (Downhower 1976, Ralls 1976); there are different uses of the wings between sexes (Mayr 1956, Jehl and Murray 1986); one sex performs acrobatic courtship displays (Jehl and Murray 1986); one sex is smaller and more maneuverable to collect nest material (Nelson 1976, Jehl and Murray 1986); a larger dominant sex maintains the pair bond (Amadon 1975, Mueller and Meyer 1985, Mueller 1986); dimorphism is correlated with predatory habits (Amadon 1959, Cade 1960); dimorphism reduces of intraspecific competition (Pitelka 1950, Selander 1966, Ashmole and Ashmole 1967); dimorphism can increase resources available (Pitelka 1950, Storer 1966); polyandry (Schamel and Tracy 1977, Jehl and Murray 1986); larger sex defends territory, nest, and young (Storer 1966, Jehl and Murray 1986); there is differential parental investment (Brown and Amadon 1968).

We try to relate these hypotheses concerning behavior, morphology, and ecology to the sexual size dimorphism in Great Frigatebirds in the central Pacific Ocean, and to the greater degree of dimorphism which exists in Christmas birds.

FRIGATEBIRD SIZE DIMORPHISM AND REVERSE SEXUAL SIZE DIMORPHISM HYPOTHESES

Jehl and Murray (1986) hypothesize that reverse sexual size dimorphism (females larger than males) develops with (1) polyandrous mating or (2) in species where the males use agility in flight to obtain a territory or attract a mate. Neither of these behavioral traits applies to Great Frigatebirds, which they acknowledge. Male Great Frigatebirds perch on a site while females fly overhead during courtship. However, they suggest that males stealing nest material, such as Nelson (1976) reports for Great Frigatebirds on Tower Island, may select for males being smaller. In 10 years of working in frigatebird colonies we have never observed either stealing of nest material from an occupied nest, or competition for nest material in any of the colonies we have studied: Johnston, Christmas, or Midway (Fairchild et al. 1985; Schreiber and Schreiber, unpubl. data). Nelson, however, did his study on Tower Island during an ENSO year, which could have dramatic effects on behavior.

We know that different uses of the wings and different capabilities in handling wind conditions do exist between sexes. Male frigatebirds do wing-waving to attract females who are flying overhead during courtship (pers. observ.; Nelson 1976) and only males collect nest material (pers. observ.; Diamond 1972), which could both be considered special uses of the wings, and thus establish a selection pressure on size as described by Mayr (1956). Harrington et al. (1972) found that female Magnificent Frigatebirds (*Fregata magnificens*) have heavier wing loading than males, and they suggested this as a reason for differences in distribution in the sexes during the nonbreeding season. Schreiber and Chovan (1986) found Great Frigatebirds to be sensitive to wind patterns. Diamond (1975) suggested that wind levels may be a factor in nest-site placement, but this cannot select for sexual dimorphism because both sexes use the same nest site. Wind levels probably affect foraging behavior and/or location, about which we know very little for this species. Selective pressures on wing dimensions, however, probably cannot be separated from those influencing other body regions or measurements. While ecological forces, such as differences in feeding between the sexes, can enhance dimorphism, it cannot be the cause (Jehl and Murray 1986).

Culmen length and wing loading differences between sexes could expand the habitat available for foraging in frigates, but preliminary analysis of regurgitation samples indicates no detectable difference between the sexes in types or sizes of food taken (Schreiber et al., unpubl.). This does not necessarily mean that both sexes are feeding in the same area. Jehl and Murray (1986), however, examined bill types in relation to sexual dimorphism in shorebirds and found no clear relationship to foraging behavior. More data are needed on feeding ecology to determine if male and female frigatebirds are actually foraging differentially. This will require at-sea observations or satellite tracking of individuals.

Kleptoparasitism is not a major food source for frigatebirds on Johnston or Christmas (Schreiber and Ashmole 1970; Schreiber et al., unpubl.), and it is done by both sexes with the same frequency, thus this behavior probably has no relationship to dimorphism.

Amadon (1975) suggested that larger, dominant females facilitate the maintenance of the pair bond in Falconiformes. Mueller and Meyer

(1985) add that this hypothesis predicts that females should be more dominant in species with a high degree of reverse sexual dimorphism. During our observations of frigatebirds over the past 20 years, we have not seen behavior that can be clearly identified as "dominance" by either sex. Aggression in defense of the nest is carried out by both sexes. In our opinion neither dominance nor aggression appear to have functional significance in shaping sexual dimorphism in frigatebirds.

Differential parental investment has been suggested as a reason for the evolution of dimorphism (Cade 1982). Diamond (1972) did find that only female Magnificent Frigatebirds feed young older than 4 months, and that female Great Frigatebirds feed fledged young more often than males. In 70 nest-days of observation of frigatebird chicks (1 week to 6 months of age) on Christmas we found no significant difference in feeding rates between males and females. Our counts of frigatebirds in colonies on Johnston and Christmas indicate an essentially equal sex ratio present at all times of the year with all ages of chicks, implying that males and females share incubation and chick rearing equally in these locations.

Mayr (1956) noted that natural selection can be particularly efficient during catastrophies and environmental stress. In spite of the 1982–1983 ENSO and resultant high mortality of adults on Christmas we have found no change in culmen, wing, or tail length, or mass before and after the ENSO event. Adults were significantly lighter in 1982 than before or after the ENSO (Table 2), probably indicating a food shortage at that time. Our finding of no change in size or mass of adults present before and after the 1982–1983 ENSO cannot be assumed to be in disagreement with Mayr's hypothesis, but indicates that it may take a series of selective barriers, such as several major ENSOs, to achieve a measurable morphological change in the population.

Christmas and Johnston are located in different oceanographic, and thus feeding, systems which could force already existing genetic divergence between populations. Christmas lies in the equatorial counter current (Wyrтки and Kilonsky 1984) near the seasonally migrating Intertropical Convergence Zone (ITCZ) (Wyrтки and Meyers 1975) and is subject to the aperiodic effect of ENSOs (Schreiber and Schreiber 1984). Frigatebirds are thought to feed north of the island

in the upwelling at the ITCZ (King and Pyle 1957; Pitman, unpubl. data). The ITCZ shifts between 4°N and 8°N on an annual cycle so that foraging areas change during the year and from year to year. Johnston is in the relatively climatologically stable north equatorial current where seasonal oceanographic changes are minimal (Wyrтки and Kilonsky 1984) and ENSO effects are much less severe (Schreiber and Schreiber, unpubl. data).

Sexual dimorphism has been suggested to be more likely to occur in an ecosystem with distinct heterogeneity (Boag and Grant 1981; Jehl, pers. comm.). Since Christmas lies in an area of unpredictable long-term oceanographic changes and seasonally fluctuating feeding areas, we consider it a heterogenous system. We would expect in such a system to see lower growth rates, lower feeding rates, and a longer period of dependency due to unpredictable, difficult feeding conditions. We have, in fact, found lower growth and feeding rates in Red-tailed Tropicbird chicks (*Phaethon rubricauda*) on Christmas (Schreiber and Schreiber, unpubl.) but still are analyzing growth data for frigatebirds.

Fledgling frigatebirds on Christmas appear to be fed by their parents longer than those on other islands: they do not become independent until 12 to 16 months (Schreiber and Ashmole 1970), but are essentially independent on Johnston at 12 months (Amerson and Shelton 1976). On other islands independence has been estimated to occur at 9 to 10 months (Stonehouse and Stonehouse 1963, Nelson 1976). We do not yet know if growth and feeding rates are lower on Christmas. Delayed fledging age could be due to oceanographic instability and thus lowered feeding rates of chicks and a greater difficulty for chicks in learning to feed. This may indicate that increased difficulty in finding food is correlated with increased sexual dimorphism. As Jehl and Murray (1986) argue, however, it is exceedingly difficult or impossible to differentiate between ecologically driven dimorphism and other types.

It is intriguing to consider that Brown Pelicans (*Pelecanus occidentalis*) have comparable social systems and breeding biology to Great Frigatebirds but they exhibit normal dimorphism with male pelicans larger than females (Palmer 1962; Schreiber et al., unpubl.). In both species males pick the nest site and display to females flying overhead, then males collect all nest material (Schreiber 1977). Pelicans lay three eggs and Great

Frigatebirds lay one, and in both species both sexes share incubation and chick rearing.

Jehl and Murray (1986) stress that an important distinction must be made between origin and function. Because sexual selection can result in ecological segregation, the differential habitat utilization that may result from sexual dimorphism may be the result of sexual selection and not specific adaptation. Sexual size dimorphism is obviously not due to the same causes in all species. Mayr (1956) stressed that the "all or none" philosophy to explain any biological phenomenon was ill-suited to evolutionary studies. Since we cannot clearly attach any of the current hypotheses on the causes of dimorphism to Great Frigatebirds, we believe we may indeed be addressing an issue for which present day ecological, morphological, and behavioral data are irrelevant.

More work is definitely needed on behavior and foraging in frigatebirds if further advances are to be made in understanding their existing morphology. Our data suggest that subspecific differentiation in Great Frigatebirds should be reexamined and that the use of canonical variates analysis techniques will enable determination of the degree of separation among various populations.

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LITERATURE CITED

- AMADON, D. 1959. The significance of sexual differences in size among birds. *Proc. Am. Philos. Soc.* 103:531-536.
- AMADON, D. 1975. Why are female birds of prey larger than males? *Raptor Research* 9:1-11.
- AMERSON, A. B., AND P. C. SHELTON. 1976. The natural history of Johnston Atoll, Central Pacific Ocean. Atoll Research Bulletin No. 192. Smithsonian Institution, Washington, DC.
- ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. *Bull. Peabody Mus. Nat. Hist.* 24: 1-131.
- BARBER, R. T., AND F. P. CHAVEZ. 1983. Biological consequences of El Niño. *Science* 222:1203-1210.
- BOAG P. T., AND P. R. GRANT. 1981. Intense natural selection in a population of Darwin's finches (*Geospizinae*) in the Galapagos. *Science* 214:82-85.
- BROWN, L., AND D. AMADON. 1968. Eagles, hawks and falcons of the world. Vol. 1. McGraw-Hill Book Co., New York.
- CADE, T. J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. *Univ. of Calif. Publ. Zool.* 63:151-290.
- CADE, T. J. 1982. The falcons of the world. Cornell Univ. Press, Ithaca, New York.
- CLIMATE DIAGNOSTICS BULLETINS. 1986-1987. El Niño Southern Oscillation (ENSO) diagnostic advisories 1985-6, 1986-6, 1987-2, 1987-3, 1987-4, 1987-5. Natl. Weather Service, NOAA, Washington, DC.
- DARWIN, C. 1871. The descent of man and selection in relation to sex. Murray, London.
- DIAMOND, A. W. 1972. Sexual dimorphism in breeding cycles and unequal sex ratio in Magnificent Frigatebirds. *Ibis* 114:395-398.
- DIAMOND, A. W. 1975. Biology and behavior of frigatebirds. *Fregata* spp. on Aldabra Atoll. *Ibis* 117: 302-323.
- DOWNHOWER, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. *Nature* 263:558-563.
- FAIRCHILD, L., S. A. MAHONEY, AND R. W. SCHREIBER. 1985. Nest material preferences of Great Frigatebirds. *J. Field. Ornithol.* 56:236-245.
- HARRINGTON, B. A., R. W. SCHREIBER, AND G. E. WOOLFENDEN. 1972. The distribution of male and female Magnificent Frigatebirds, *Fregata magnificens*, along the Gulf Coast of Florida. *Am. Birds* 26:927-931.
- HARRISON, P. 1983. Seabirds, an identification guide. Houghton Mifflin Co., Boston.
- JAMES, F. C. 1970. Geographic variation in birds and its relation to climate. *Ecology* 51:365-390.
- JEHL, J. R., JR., AND B. G. MURRAY, JR. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds, p. 1-76. *In* R. F. Johnson [ed.], *Current ornithology*. Vol. 3. Plenum Press, New York.
- KING, J. E., AND R. L. PYLE. 1957. Observations of seabirds in the tropical Pacific. *Condor* 59:27-39.
- MAYR, E. 1956. Geographical character gradients and climatic adaptation. *Evolution* 10:105-108.
- MAYR, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, MA.
- MAYR, E., AND G. W. COTTRELL [EDS.]. 1979. Checklist of birds of the world. Vol. 1. 2nd ed. Museum of Comparative Zoology, Cambridge, MA.
- MUELLER, H. C. 1986. The evolution of reverse sex-

- ual dimorphism in owls: an empirical analysis of possible selective factors. *Wilson Bull.* 98:387-406.
- MUELLER, H. C., AND K. MEYER. 1985. The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the western Palearctic. In R. F. Johnston [ed.], *Current ornithology*. Vol. 2. Plenum Press, New York.
- NELSON, J. B. 1976. The breeding biology of frigatebirds—a comparative review. *Living Bird* 14: 113-155.
- OLSON, S. L. 1977. A lower Eocene frigatebird from the Green River formation of Wyoming (Pelecaniformes: *Fregatidae*). *Smithson. Contrib. Paleobiol.* 35:1-33.
- PALMER, R. S. 1962. *Handbook of North American birds*. Vol. 1. Yale Univ. Press, New Haven.
- PAYNE, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.* No. 33. American Ornithologists' Union, Washington, DC.
- PITELKA, F. A. 1950. Geographic variation and the species problem in the shore-bird genus *Limnodromus*. *Univ. of Calif. Publ. Zool.* 50:1-108.
- POWER, H. W. 1980. The foraging behavior of Mountain Bluebirds, with emphasis on sexual foraging differences. *Ornithol. Monogr.* No. 20. American Ornithologists' Union, Washington, DC.
- RALLS, K. 1976. Mammals in which females are larger than males. *Q. Rev. Biol.* 51:245-276.
- SCHAMEL, D., AND D. TRACY. 1977. Polyandry, replacement clutches and site tenacity in the Red Phalarope (*Phalaropus fulicarius*) at Barrow, Alaska. *Bird-Banding* 48:314-324.
- SCHREIBER, R. W. 1977. Maintenance behavior and communication in the Brown Pelican. *Ornithol. Monogr.* No. 22. American Ornithologists' Union, Washington, DC.
- SCHREIBER, R. W., AND N. P. ASHMOLE. 1970. Seabird breeding seasons on Christmas Island, Pacific Ocean. *Ibis* 112:363-394.
- SCHREIBER, R. W., AND J. L. CHOVAN. 1986. Roosting by pelagic seabirds: energetic, populational and social considerations. *Condor* 88:487-492.
- SCHREIBER, R. W., AND E. A. SCHREIBER. 1984. Central Pacific seabirds and the El Nino Southern Oscillation: 1982-1983 perspectives. *Science* 225: 713-716.
- SELANDER, R. K. 1966. Sexual dimorphism and niche utilization in birds. *Condor* 68:113-151.
- STONEHOUSE, B., AND S. STONEHOUSE. 1963. The frigatebird *Fregata aquila* of Ascension Island. *Ibis* 103:409-422.
- STORER, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. *Auk*: 423-436.
- WYRTKI, K., AND B. KILONSKY. 1984. Mean water and current structure during the Hawaiian-to-Tahiti shuttle experiment. *J. Physical Oceanography* 14:242-254.
- WYRTKI, K., AND G. MEYERS. 1975. The trade wind field over the Pacific Ocean, Part 1, The mean field and the mean annual variation. Hawaii Institute of Geophysics, Univ. of Hawaii, Honolulu.