

Sexual dimorphism, extrapair fertilizations, and operational sex ratio in great frigatebirds (*Fregata minor*)

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Across taxa, the presence of sexual ornaments in one sex is usually correlated with disproportionately great parental effort by the other. Frigatebirds (Fregatidae) are sexually dimorphic, with males exhibiting morphological and behavioral ornaments, but males and females share in all aspects of parental effort. All other taxa in a clade of 237 species exhibit biparental care, but only frigatebirds exhibit pronounced sexual dimorphism. We tested for the presence of two factors that could contribute to the evolution of male ornaments in great frigatebirds: a high frequency of extrapair fertilizations and a male-biased operational sex ratio. In 92 families sampled over two breeding seasons, there was only one extrapair fertilization. However, in both seasons, there were more males than females available for mating, and the sex ratio among individuals actively engaged in mate-acquisition behavior was strongly male biased, with typically five or six males available per female. Our results suggest that extrapair fertilizations are not responsible for the exaggeration of sexual ornaments in male frigatebirds, and that operational sex ratio may be related to sexual dimorphism in this species. Further work is needed to determine whether the male-biased operational sex ratio creates the variance in male reproductive success that would be needed to drive the evolution of male ornaments. *Key words:* extrapair fertilizations, *Fregata minor*, frigatebirds, operational sex ratio, ornaments, sexual dimorphism, sexual selection. [*Behav Ecol* 12:746–752 (2001)]

Across taxa, sexual selection theory predicts that the presence of exaggerated secondary sexual traits in one sex should correlate with mate choice and disproportionately great parental effort by the other sex (Andersson, 1994). Thus, for species in which males possess extravagant ornaments, females typically exert mate choice and subsequently provide most or all of the parental care. In contrast, species that lack sexual ornaments are often characterized by balanced parental effort by males and females. Part of the explanation for this relationship is that if males do not contribute to parental care, their reproductive success becomes more heavily dependent on their mating success, leading to more intense male–male competition or more selective female choice; these pressures can, through a variety of mechanisms, lead to the evolution of male sexual ornaments.

The positive relationship among male ornaments, female choice, and female parental care holds true especially among birds (Andersson, 1994). However, frigatebirds (Fregatidae) depart from this pattern. Male frigatebirds exhibit exaggerated secondary sexual traits not shared by females, including an inflatable red throat pouch and an iridescent ruff of feathers. These traits are highlighted by extravagant courtship displays, in which a male inflates the throat pouch, erects his iridescent ruff, tilts and wags his head, outstretches and trembles his wings, and vocalizes (Nelson, 1975). These displays are performed in large groups at which females can assess hundreds of potential mates at once (Nelson, 1975). Despite

this leklike mate choice, males and females form social pair bonds, and males invest heavily in parental care. Males gather all of the nest material (Nelson, 1975; Dearborn, unpublished data), they incubate for almost half of the 57-day incubation period (Dearborn, 2001), they share in brooding the chick for 4–6 weeks (Nelson, 1975; Dearborn and Anders, unpublished data), and they contribute extensively to feeding the chick for approximately 8 months (Nelson, 1975; Dearborn and Anders, unpublished data).

Because this combination of pronounced sexual dimorphism and balanced parental effort by males and females is unusual from a life-history standpoint, it is insightful to use a phylogenetic framework for considering the presence of these traits in frigatebirds. By mapping sexual dimorphism and balanced parental effort onto a phylogeny built with mitochondrial 12S–16S rRNA and cytochrome B sequence data (Siegel-Causey, 1997), one can see that biparental care is a completely conserved ancestral trait in this clade of more than 200 species but that pronounced sexual dimorphism is a derived trait found only in the 5 species of frigatebirds (Figure 1). This same result is obtained by mapping these characters onto phylogenies based on morphology (Cracraft, 1985), mitochondrial rRNA sequence data (Hedges and Sibley, 1994), DNA–DNA hybridizations (Sibley and Ahlquist, 1990), or a combination of behavioral and morphological traits (Siegel-Causey, 1997). Thus, when considering the unusual combination of male sexual ornaments and balanced parental effort in frigatebirds, it seems most appropriate to ask why male frigatebirds may have evolved sexual ornaments.

One force that may have driven the evolution of male sexual ornaments in frigatebirds is females' interest in, and ability to obtain, extrapair fertilizations (i.e., fertilizations by males other than their social mates). Over the past 15 years, researchers have come to realize that extrapair fertilizations are prevalent in many species of birds (Fleischer, 1996; Gowaty, 1996; Westneat and Sherman, 1997), and this revelation has dramatically changed our view of avian mating systems and

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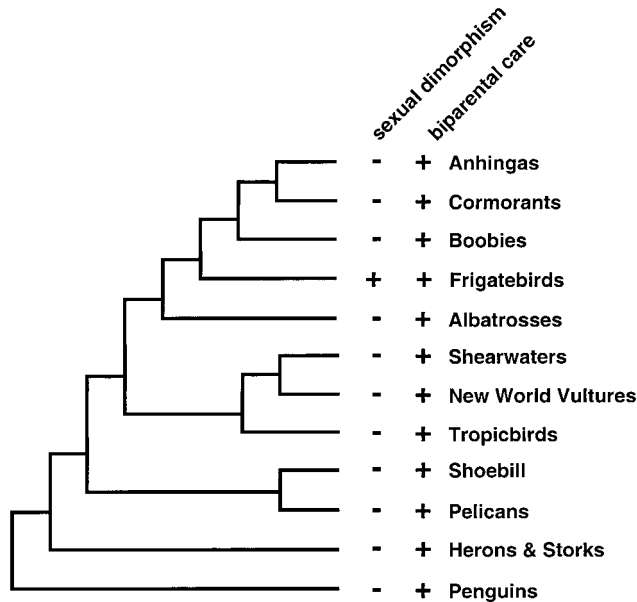


Figure 1

Phylogeny of frigatebirds and related taxa, based on sequence data from three mitochondrial genes (12S rRNA, 16S rRNA, and cytochrome b; Siegel-Causey, 1997). All taxa (13 families totaling 237 species) are characterized by biparental care, but only the five frigatebird species exhibit pronounced sexual dimorphism. Results of trait mapping are the same using phylogenies based on morphology (Cracraft, 1985), mitochondrial rRNA sequence data (Hedges and Sibley, 1994), DNA-DNA hybridizations (Sibley and Ahlquist, 1990), or a combination of behavioral and morphological traits (Siegel-Causey, 1997).

sexual selection (Parker and Burley, 1998; Petrie and Kempenaers, 1998). Variation between species and between populations in the frequency of extrapair fertilizations has been linked to a wide array of ecological, behavioral, and morphological factors, including the degree of breeding synchrony (Stutchbury and Neudorf, 1998), the clustering of breeding territories or the formation of colonies (Wagner, 1998), and the presence of bright male plumage (Møller and Birkhead, 1994). The work by Møller and Birkhead (1994) showed that, across species, degree of male plumage brightness was positively correlated with frequency of extrapair fertilizations. Extrapair fertilizations are generally rare in seabirds (Austin and Parkin, 1996; Hunter et al., 1992; Mauck et al., 1995; Schwartz et al., 1999; Swatschek et al., 1994; but see Huyvaert et al., 2000). Thus, the uniquely derived sexual dimorphism seen in frigatebirds could be driven by an unusually high rate of extrapair fertilizations.

A second possible driving force in the exaggeration of male traits in frigatebirds is a male-biased operational sex ratio. At any given time, there may be more males available for mating than there are females, leading to female choosiness or male-male competition (Kvarnemo and Ahnesjö, 1996). A biased operational sex ratio has been shown to drive sexual selection in many organisms, including insects (Kvarnemo and Simmons, 1999), frogs (Wagner and Sullivan, 1992), snakes (Weatherhead et al., 1995), fish (Kodric-Brown, 1988; Balshine-Earn, 1996), and birds (Colwell and Oring, 1988).

The mechanism linking male sexual ornaments to either a high rate of extrapair fertilizations or a male-biased operational sex ratio is one of heightened variance in male reproductive success and thus stronger sexual selection on males (e.g., Yezerinac et al., 1995). Under the extrapair fertilization hypothesis, variance in male reproductive success would result

from females preferring a subset of males as fertilization partners; under the operational sex ratio hypothesis, variance in male reproductive success would result from differential male success at attracting a social mate. In this study, we determined whether a high rate of extrapair fertilizations or a male-biased operational sex ratio exists in a population of great frigatebirds, and thus whether either of these factors has the potential to drive male variance in reproductive success in this species.

METHODS

Study area and species

We conducted this study of great frigatebirds on Tern Island, French Frigate Shoals (23°45' N, 166°17' W), in the northwestern Hawaiian Islands. Tern Island is approximately 14 ha and is a breeding area for 15 species of seabirds totaling more than 200,000 individuals (see Amerson, 1971, for more details). Roughly 4000 adult frigatebirds come to Tern Island during the breeding season (Dearborn et al., unpublished data). The nearest neighboring colony of breeding frigatebirds occurs on Laysan Island, approximately 600 km northwest of Tern Island.

On Tern Island, male great frigatebirds begin performing courtship displays in January, and egg laying typically lasts from early February through late May. Groups of males display from perch sites in bushes (primarily *Tournefortia* spp.), and females fly above the colony, making initial inspections of males from the air. A female will then land beside a male to perform what appears to be a closer inspection, during which the male usually intensifies his display behavior. If the female accepts the male, they spend several days perched in close proximity to each other before they begin constructing the nest. The interval from initial pair formation to egg laying is typically 1–2 weeks. The total duration of parental care by frigatebirds is approximately 1 year and is among the longest for all species of birds. In addition, adult frigatebirds are very long-lived; there are individuals in our study population that are 37 years old (Dearborn et al., unpublished data).

Extrapair paternity

To measure the frequency of extrapair paternity, we collected blood samples from 62 social families in 1998 and 30 families in 1999. In 1998, 21 of the 62 families were from nests that we were monitoring to collect detailed data on parental effort (Dearborn, 2001); the remaining 41 families in 1998 were randomly chosen from throughout the colony, and we spread our overall sample of nests across the breeding season. Tern Island is elongated (roughly 1 km by 200 m), bisected along its long axis by a sand runway, and marked with a short-axis grid every 10 m from 0 to 970 m. To choose a family from which to obtain blood samples, we randomly selected the north or south side of the runway, randomly chose a number from 0 to 970, and then chose the closest nest to that meter marker that contained a chick old enough from which to obtain a blood sample. Due to a shorter 1999 field season, in 1999 we sampled the 30 earliest nests of the season that were successful long enough for us to obtain blood samples (roughly 3 weeks after hatching). In both years, all blood samples were collected when chicks were still being constantly brooded to ensure that adults that we sampled were truly the social parents. We collected two 50- μ l blood samples from each individual from the leg or foot, and samples were stored in a lysis buffer (Longmire et al., 1988).

To assess the frequency of extrapair fertilizations, we used multilocus minisatellite fingerprinting, using the protocol of

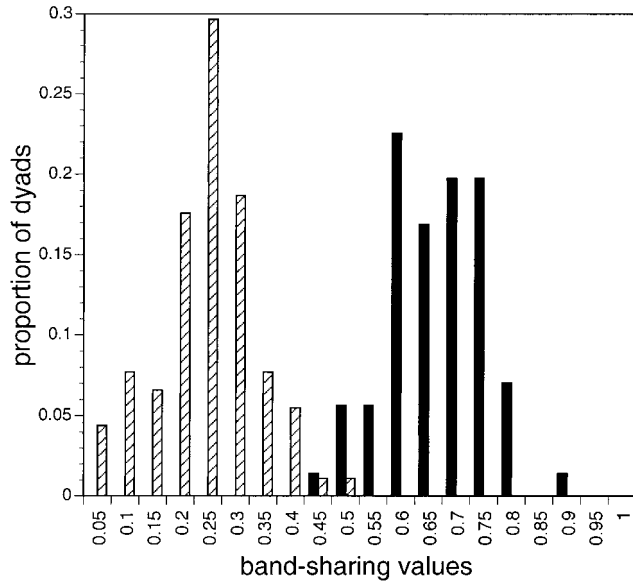


Figure 2
Frequency distribution of band-sharing coefficients for dyads of a chick with one of its parents (filled bars) and for dyads of a chick with a putatively unrelated adult from a different social family (hatched bars). In this graph, chick-parent dyads were restricted to those chicks with zero unattributable bands.

Parker et al. (1994). Following extraction, DNA was digested with *HaeIII*. The resulting fragments were separated on agarose gels, blotted to nylon, and subsequently hybridized with Jeffreys's probe 33.15 (Jeffreys et al., 1985a,b).

Because a single egg is laid during a breeding attempt, each family group consists of a male, a female, and a single chick. For each chick, we counted the number of bands that were not attributable to either of its putative parents. Second, we calculated a band-sharing index for dyads of chicks and their putative parents. Band sharing was defined as $2S/(A + B + 2S)$, where S = number of bands shared by the pair of birds, A = number of bands unique to bird A, and B = number of bands unique to bird B (Wetton et al., 1987). Next, we assessed the extent of overlap in band-sharing values between putative first-order relatives and putative nonrelatives. To obtain dyads of nonrelated birds, we paired each chick's lane with the lane of an adult from an adjacent family on the same gel. The sex of the unrelated adult was chosen randomly. Birds paired in this way were usually one or two lanes apart on the digestion gel. For comparison of the distribution of the band-sharing scores of pairs of related and unrelated birds, we restricted our parent-offspring dyads to those families in which there were zero unattributable bands ($n = 71$), and we randomly selected one of the parents for each chick. Thus, for this comparison each chick was used once in a dyad with one of its parents and once in a dyad with a nonparent from a nearby lane.

Using the resulting distribution of band-sharing values (Figure 2), we defined a cutoff of mean + 1.96 SD = $0.220 + 1.96(0.090) = 0.398$ as the upper limit for band-sharing values by unrelated birds. We marked this cutoff on a graph of band-sharing score versus number of unattributable bands, plotting separate points for chick-mother dyads and for chick-father dyads (Figure 3). Chicks falling below this band-sharing threshold and having more than two unattributable bands were classified as extrapair young.

We calculated the mutation rate by counting the average number of novel fragments detected in all nonexcluded

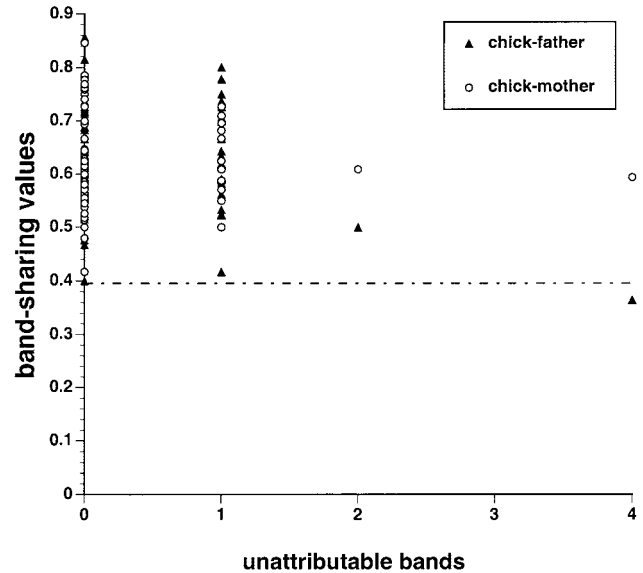


Figure 3
Band-sharing scores between a chick and each of its social parents plotted versus number of unattributable bands in the chick's DNA fingerprint. Horizontal line indicates the upper cutoff for band-sharing between unrelated birds, based on mean band-sharing + 1.96 SD. The only chick falling below this cutoff had more than two unattributable bands, indicating that this chick was sired by a male other than its social father. Thus, the frequency of extrapair fertilizations in our sample was 1 in 92 (1.1%).

chicks and dividing this by the average number of fragments scored per chick. We used a one-sample Kolmogorov-Smirnov test to test whether the observed number of offspring having zero, one, or two novel fragments differed from the corresponding frequencies expected under a Poisson distribution.

Operational sex ratio

We used two different measures of operational sex ratio (OSR). We defined the general OSR as the ratio of available males to females based on the number of sexually mature adults that were at the breeding colony but were not occupying nests. Data from hundreds of individually marked birds clearly indicate that birds whose mates are incubating do not spend time at the breeding colony while off the nest; rather, these birds fly away from the island to forage, and when they return to the colony they go directly to the nest to relieve their incubating mates. Thus, if a bird is at the colony but is not currently occupying a nest, it does not have a nest that is being tended by a mate.

In both 1998 and 1999, we measured the general OSR daily at 1730 h HST. At this time of day, birds in the colony are very active. Although some species of seabirds on Tern Island (e.g., red-footed boobies, *Sula sula*) exhibit pronounced diurnal variation in colony attendance, exploratory counts of frigatebirds conducted multiple times per day did not detect consistent variation in colony attendance over the course of the day.

Our counts of general OSR were made by taking the same route around the breeding colony each day, and our search path was never more than 50 m from the birds that we were counting. Frigatebirds are large animals (2-m wingspan) that perch on the tops of low bushes (generally 1 to 2 m high), and Tern Island is treeless and sparsely vegetated. Thus, detection of individuals during a count is not difficult. Daily counts were conducted by the same individual (D.C.D.) over

both seasons. Because the number of birds that were flying during our counts was small relative to the total number of individuals being counted (6%), the likelihood of double counting a meaningful number of individuals over the 45 min that it took the observer to circle the colony is small.

In 1999, we included an additional measure of sex ratio, the immediate OSR. This was quantified by counting males that were currently performing mate-attraction behaviors and females that were currently involved in mate-searching or mate-evaluating behaviors. Male courtship display consists of many behavioral elements, including gular pouch inflation, head tilting, head wagging, wing fluttering, and vocalizations, but inflation of the gular pouch is the one component common to all levels of involvement in display behavior (Dearborn et al., unpublished data). Thus, a male was included in the immediate OSR if his gular pouch was partially or fully inflated. Mate choice by females primarily involves two stages: first, a female makes low flights over the colony making conspicuous visual inspections of displaying males below; second, a female lands and perches next to a male for further evaluation. Thus, a female was included in the immediate OSR if she was performing mate-inspection flights or if she was perched in physical contact with a male who was not on a nest. The immediate OSR was counted by a second observer (A.D.A.) at the same time as the general OSR and using the same route around the colony.

RESULTS

Extrajair paternity

The DNA fingerprints from 90 of 92 (97.8%) chicks had 0 or 1 bands that were unattributable to the chick's social parents. The frequency distribution of the number of unattributable bands did not differ from expected frequencies based on a Poisson distribution (Kolmogorov-Smirnov $Z = 0.131$, $p = 1.00$). The average number of novel bands per chick was 0.231, and the average number of bands scored per chick was 14.1, yielding a mutation rate of 0.0164 per locus per meiotic event, a value within the range of those found for minisatellite markers in other seabird species (0.008: Mauck et al., 1995; 0.0145: Schwartz et al., 1999; 0.017: Hunter et al., 1992; 0.024: Austin and Parkin, 1996). Based on the Poisson distribution, the probability of a chick having three or more unattributable bands from mutation alone is 0.0017.

There was minimal overlap between the band-sharing scores for dyads of chicks with their putative parents and dyads of chicks with unrelated adults (Figure 2). Only one chick had a score below the 0.398 cutoff used to delineate the upper limit for band-sharing of unrelated birds, and this chick had four unattributable bands (Figure 3). Band-sharing between this chick and its mother was 0.594, whereas band-sharing with its father was 0.364, indicating that this chick was sired by a male other than its social father. To confirm this result, we extracted DNA from the backup blood samples for this family and repeated the genetic analysis; the male was still excluded as the sire of the chick. A chick from another family had two unattributable bands, but its band sharing was 0.609 with its mother and 0.500 with its father. The frequency of extrajair fertilizations in our sample was thus 1 in 92 (1.1%). Because frigatebirds lay a single egg, the rate per chick and rate per family are the same.

Operational sex ratio

In both years, the general OSR (based on the number of adults at the colony that were not occupying nests) was male biased over the pair-formation and egg-laying portion of the

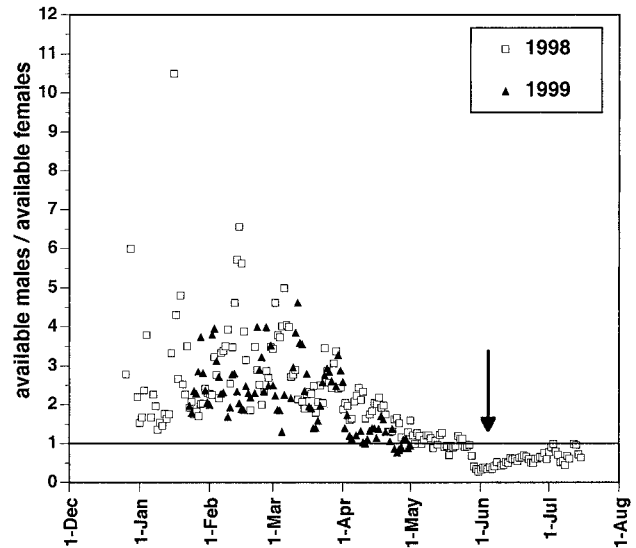


Figure 4

The general operational sex ratio, defined by the ratio of adult males to adult females at the breeding colony but not occupying nests, was male biased over the pair-formation and egg-laying part of the breeding season in both 1998 and 1999. The arrow marks the date at which the last egg was laid in the 1998 season, but in both years male courtship displays and pair formation tapered off in April.

breeding season (Figure 4). Typically, there were two to three males available per female, and there was striking similarity in the general OSR between years. As courtship displays tapered off in April, the general OSR became balanced and, eventually, female biased. The immediate OSR, measured during the pair-formation and egg-laying portion of the 1999 season, was even more male-biased than the general OSR—typically five or six displaying males for each female engaged in mate evaluation. Unlike the general OSR, the immediate OSR did not exhibit a seasonal decline (Figure 5).

DISCUSSION

In this study, we found a low rate of extrajair fertilizations in a population of great frigatebirds, indicating that extrajair fertilizations likely do not play a role in driving the exaggeration of male sexual ornaments seen in this species. We did, however, find a strongly male-biased operational sex ratio. This male-biased sex ratio has the potential to select for male sexual ornaments, although a causal link between these factors remains to be established.

Extrajair paternity

Several observations during this study led us to anticipate a relatively high frequency of extrajair fertilizations in great frigatebirds. First, of the dozens of copulations that we witnessed, several were known to be extrajair. Two of these extrajair copulations were conspicuous and two involved a female great frigatebird and a male lesser frigatebird (*F. ariel*; Dearborn and Anders, 2000). It is unlikely that extrajair copulations (EPCs) frequently involve lesser frigatebirds; rather, heterospecific extrajair copulations were much more likely to be opportunistically noted by observers than were conspecific EPCs because lesser frigatebirds were rare on Tern Island (Dearborn and Anders, 2000) and there were no mixed-species social pairs. Regardless of the relative frequency of conspecific and heterospecific EPCs, it is clear that some female

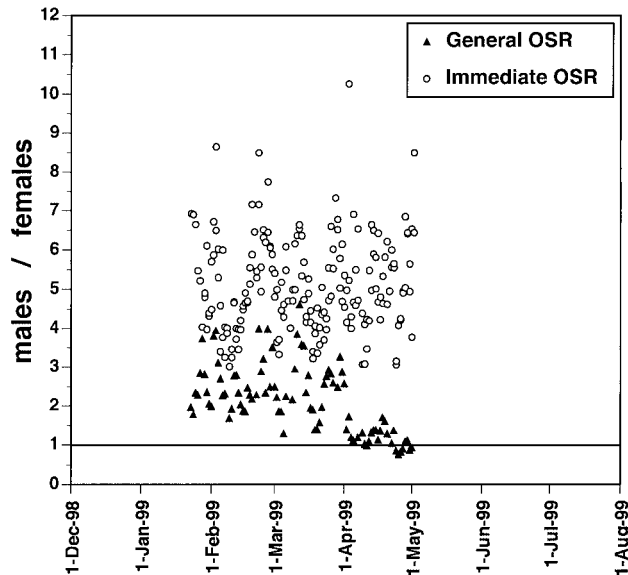


Figure 5
In 1999, the immediate operational sex ratio, defined by the number of adult males performing courtship displays and the number of adult females involved in mate-searching and mate-evaluating behaviors, was more strongly male-biased than the general operational sex ratio.

great frigatebirds do engage in EPCs. Second, unlike many Passerines, male frigatebirds cannot guard their mates during the female's fertile period because unattended nests will be dismantled by other males competing for nest material. Because a male could not follow his mate when she left the nest to forage during her fertile period, the male could neither prevent EPCs nor assess his likelihood of paternity. Third, within the 14-ha colony, hundreds of males were potentially available as EPC partners. Fourth, male frigatebirds have exaggerated secondary sex traits, and the presence of such ornaments is often correlated with a high frequency of EPFs (Møller and Birkhead, 1994). Although constraints on mate guarding are not unusual among seabirds, the presence of sexual ornaments is unique to frigatebirds, prompting our initial hypothesis that frequent extrapair fertilizations may occur in frigatebirds.

In contrast to these expectations, we found a low frequency of extrapair fertilizations in frigatebirds (1 chick out of 92; 1.1%). This result is consistent with the predictions of a recent model (Mauck et al., 1999) and with most empirical studies of seabirds that lack the strong sexual dimorphism seen in frigatebirds. Previous empirical work with seabirds has shown a low frequency of extrapair fertilizations for northern fulmars, *Fulmarus glacialis* (0%; Hunter et al., 1992), short-tailed shearwaters, *Puffinus tenuirostris* (9–13%; Austin and Parkin, 1996), Cory's shearwaters, *Calonectris diomedea* (0%; Swatschek et al., 1994), Leach's storm-petrels, *Oceanodroma leucorhoa* (0%; Mauck et al., 1995), common murre, *Uria aalge* (8%; Birkhead et al., 2001), Humboldt penguins, *Spheniscus humboldti* (0%; Schwartz et al., 1999), royal penguins, *Eudyptes schlegeli* (4%; St. Clair et al., 1995), and chinstrap penguins, *Pygoscelis antarctica* (0%; Moreno et al., 2000). Higher frequencies of extrapair fertilizations have been noted in two seabirds, the shag, *Phalacrocorax aristotelis* (18%; Graves et al., 1992), and the waved albatross, *Phoebastria irrorata* (25%; Huyvaert et al., 2000). Interestingly, northern fulmars (Hunter et al., 1992) and Humboldt penguins (Schwartz et al., 1999) both exhibit low rates of extrapair fertilizations despite frequent EPCs. In fulmars, males appear to prevent cuckoldry

by performing frequent within-pair copulations. In Humboldt penguins and also in razorbills (*Alca torda*), many EPCs are solicited by females outside of their fertile period (Schwartz et al., 1999; Wagner, 1991), suggesting that these copulations may serve to facilitate appraisal and acquisition of future mates, as originally proposed by Colwell and Oring (1989). In great frigatebirds, the exact frequency and function of EPCs remains to be determined, but extrapair fertilizations clearly are not common. Despite the apparent impact of high extrapair fertilization rates on the evolutionary ecology of other groups of birds (Fleischer, 1996; Gowaty, 1996; Møller and Birkhead, 1994), sexual selection via extrapair paternity does not appear to be a major force shaping the mating systems of seabirds in general or frigatebirds in particular.

Operational sex ratio

The general OSR, defined by the number of unpaired adult males and females at the breeding colony, was male biased over the mate-choice portion of the breeding season in both years. The scale and pattern of the general OSR were strikingly similar in the 2 years, suggesting that the presence and extent of a male-biased OSR may be a general feature of this system. Limited data from other populations suggest that a male-biased OSR may be widespread among great frigatebirds (Diamond, 1975; Reville, 1983). The decline in general OSR late in the season was due primarily to an increase in the number of females on the island. The status of these females (whether they were nonbreeders, birds whose nests had already failed, etc.) was not known, making it difficult to interpret the change in general OSR.

The more relevant measure of sex ratio, from the standpoint of sexual selection, is the immediate OSR. The immediate OSR, defined as the ratio of males to females currently participating in mate-acquisition behaviors, was even more strongly male biased than was the general OSR. Moreover, the ratio of displaying males to mate-seeking females remained strongly male biased over the entire time that birds were seeking mates and starting nests. Such a skew in the ratio of males and females that are ready to mate is often correlated with other measures of intensity of sexual selection (e.g., Colwell and Oring, 1988).

An important next step in our system is to assess whether this male-biased OSR does indeed lead to large variance in male reproductive success. Such variance is most likely to arise via female choice, as males rarely compete overtly for display sites or nest sites, whereas females make careful physical inspections of males during mate choice. If the biased immediate OSR reflects an underlying skew in the numbers of males and females attempting to mate in a given season, variance in male pairing success might be a large component of male variance in overall reproductive success. In this case, males with more exaggerated sex traits would be expected to be more successful at attracting a mate. In contrast, if the immediate OSR reflects behavioral differences between males and females (rather than a skew in the number of birds trying to breed in a given season), variance in male reproductive success is more likely to be a result of variance in nesting success of mated males. This could occur in at least two ways: (1) males with more exaggerated traits might attract better quality or better condition females as mates, or (2) males with more exaggerated traits might attract a mate earlier in the season, with earlier mating being advantageous independent of mate quality. An alternative class of explanations is that the male-biased OSR is a behavioral consequence, rather than a cause, of strong sexual selection on males.

Understanding the relationship among OSR, sexual selection, and male ornaments will require knowledge of the

mechanism underlying the skewed OSR. Demographic mechanisms, such as a skewed sex ratio at hatching or differential male and female mortality, are possible. However, because the general OSR declined over the season, while the immediate OSR remained constant and more strongly male biased, a behavioral explanation is more likely. Behavioral mechanisms could be of two types: there may be differences in time budgets of the males and females that are trying to breed in the current year, or males and females may differ in the frequency with which they attempt to breed. This last possibility has been the subject of much speculation in the literature over the past 30 years (Carmona et al., 1995; Diamond, 1972, 1973; Nelson, 1975; Trivelpiece and Ferraris, 1987). Diamond (1972) hypothesized that males cease providing care for their chicks early enough to attempt to breed annually, whereas females continue feeding chicks for a long enough time period that they cannot attempt to breed during the year following a successful nest. Of the five frigatebirds species, only magnificent frigatebirds (*Fregata magnificens*) seem to exhibit this pattern of early male abandonment (Osorno, 1999), but additional information on the duration of parental care and on the frequency of breeding attempts by males and females is needed for the four other species.

The overall adult sex ratio in birds is often slightly male biased (typically 1.2 to 1.8 males/female among monogamous species; Breitwisch, 1989), but comparative data on OSR are generally scant. Measures of sex ratios in Pelecaniformes and their allies are largely unavailable, because all other members of this clade lack pronounced sexual dimorphism, and thus sex cannot be determined by plumage. Among the few species for which adult sex ratio data do exist, there is no evidence for a markedly male-biased sex ratio (brown booby, *Sula leucogaster*: Gilardi, 1992; Tershly and Croll, 2000; Western grebe, *Aechmophorus occidentalis*: Nuechterlein and Buitron, 1998; Buller's albatross, *Diomedea bulleri*: Stahl et al., 1998; Galapagos cormorant, *Compsohalieus harrisi*: Valle, 1995; great cormorant, *Phalacrocorax carbo*: Van Eerden and Munsterman, 1995). More detailed sex ratio data are needed for this clade, and the recent advent of a broadly-applicable sex-specific molecular marker (Griffiths et al., 1998) will make such advances possible.

In summary, we found a low frequency of extrapair fertilizations, but a strongly male-biased OSR, in this population of great frigatebirds. The infrequency of extrapair fertilizations is unusual from the standpoint of male ornaments and female opportunity but not from the standpoint of life history traits. A strongly male-biased OSR has the potential to be a selective force driving the unique derivation of male sexual ornaments in frigatebirds; previous studies have demonstrated a positive relationship between skew in OSR and strength of sexual selection (Kvarnemo et al., 1995; Lawrence, 1986). Additional work is needed to determine whether the skewed OSR in this system leads to variance in male reproductive success. Comparative OSR data from other frigatebird species and from monomorphic Pelecaniformes would also provide information on the relationship between a skewed OSR and sexual dimorphism in these species.

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