

Body condition and retaliation in the parental effort decisions of incubating great frigatebirds (*Fregata minor*)

Donald C. Dearborn

Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, USA

Decisions about parental effort have the potential to be affected by an individual's body condition and, among species with biparental care, by the level of effort made by one's mate. Previous studies, primarily of short-lived species, have found that a reduction in the parental effort of one pair member typically leads to a compensatory increase by the mate. However, long-lived species with short-term pair bonds might be expected to retaliate, rather than compensate, for a reduction in a mate's effort. I studied the factors affecting parental effort decisions during incubation by the great frigatebird, a long-lived seabird that forms new pair bonds for each breeding attempt. During incubation, males and females took turns incubating and foraging. Individuals lost mass during an incubation shift and regained this mass during the subsequent foraging bout. If an individual was left on the nest for a long period of time while its mate was foraging, it subsequently went on a long foraging trip after being relieved by its mate, despite the fact that longer shifts were likely to lead to nest failure. This relationship between incubation shift length and duration of subsequent foraging excursion could be due to a need to regain body condition after a long fast, or it could reflect a retaliatory response to the mate's prolonged absence. To test these alternatives, I conducted a food supplementation experiment. Individuals engaged in a long incubation shift were assigned to a control group or to a treatment group that was fed until the end of that particular incubation shift. Overall, fed birds returned from the subsequent foraging trip sooner than control birds, demonstrating that the relationship between incubation shift duration and foraging trip duration is due primarily to a need to increase body mass, rather than being a retaliatory response to a mate's low level of parental effort. However, males and females differed in the extent of their responses to the experimental treatment, indicating that males may also exhibit some degree of retaliation. *Key words:* body condition, *Fregata*, frigatebird, incubation, parental effort, Prisoner's Dilemma, retaliation. [*Behav Ecol* 12:200–206 (2001)]

Decisions about the allocation of parental effort may be affected by a wide array of factors. For iteroparous organisms, decisions about how much effort to expend on the current breeding attempt can be governed, in part, by the individual's current body condition, such that individuals in poor condition may reduce their current effort to avoid jeopardizing survival and future reproductive attempts (Chastel et al., 1995; Erikstad et al., 1997; Olsson, 1997).

Among species with biparental care, decisions about the allocation of parental effort may also depend on the level of effort put forth by one's mate (Houston and Davies, 1985). If one's mate reduces its parental effort, an individual can adjust its own effort in one of two ways. On one hand, it might increase its effort to offset the reduction in the mate's effort. Indeed, an array of mate-removal and mate-handicapping experiments have shown that compensation (i.e., an increase in effort) is a common response to reduced effort by one's mate (e.g., Saino and Møller, 1995; Sasvari, 1986). However, this compensation is often incomplete, such that the increase in parental effort by one individual does not completely make up for the low level of effort by the mate (Markman et al., 1995; Wright and Cuthill, 1989).

An alternative response is for an individual to reduce its effort in "retaliation" for lowered effort by its mate. Retaliation, in such a situation, would be defined as a reduction in

an individual's parental effort following a low relative level of effort by the individual's mate. No study has yet demonstrated a negative response to mate's reduced effort. However, Wright and Cuthill (1989) raised the possibility that the incompleteness of the parental effort compensation seen in many species may not be due to energetic or survival limitation, but may instead reflect a countermeasure against the individual's mate.

To date, most studies of the adjustment of parental effort in response to mate's effort have been conducted with short-lived species. Because these species have limited lifetime breeding opportunities, individuals may be expected to partially or fully compensate, rather than retaliate, in response to low levels of parental effort by the mate (Williams, 1966). Of the few studies conducted with long-lived species, all have been of species with long-term pair bonds (Tverra et al., 1997; Weimerskirch et al., 1995). In such species, pair bond duration can increase reproductive success (Cézilly and Nager, 1996; Choudhury, 1995); thus, the pressure to maintain a successful relationship with one's long-term mate may offset any potential benefits of retaliation. Retaliation would be most likely to occur in iteroparous species with short-term pair bonds, in which retaliation would be unlikely to affect future pairing and reproductive success.

Great frigatebirds (*Fregata minor*, Family *Fregatidae*) provide an interesting system for evaluating the relative importance of body condition and retaliation in parental effort decisions. Great frigatebirds are long-lived seabirds (maximum age ≥ 37 years in my study population), but unlike most seabirds, male and female frigatebirds pair with different mates between years (Nelson, 1975; Reville, 1988) and they will even re-pair with different mates during the same breeding season

Address correspondence to D. Dearborn, who is now at Department of Biology, Southwestern University, P.O. Box 770, Georgetown, TX 78627-0770. E-mail: dearbord@southwestern.edu.

Received 2 August 1999; revised 28 July 2000; accepted 21 August 2000.

following nest failure (personal observation). Despite the temporary nature of the partnership between great frigatebird mates, the duration of parental care by both male and female great frigatebirds is among the longest of all birds, with an incubation period of 57 days and a juvenile care period of approximately 12 additional months.

To study factors affecting the parental effort decisions of great frigatebirds, I used incubation shift length as a measure of parental effort. Incubation shift length is a good assay of parental effort in frigatebirds because the incubation period critically determines reproductive success as this stage of breeding generally exhibits the highest rate of nest failure in seabirds (Prince et al., 1994), and because incubation shift lengths can be quantified more robustly than can parental contributions to chick rearing. In considering the dynamics of incubation shifts by great frigatebirds, it is important to bear in mind that the duration of a particular incubation shift is governed not by the incubating bird, but by the return-to-the-nest decisions of the mate, who is currently foraging. Such decisions could be based on the forager's recovery of body mass (to maintain adequate body condition) or on the amount of parental effort made thus far by the bird's mate (i.e., a retaliatory response to the mate's parental effort). The interactions between mates during incubation could thus be viewed as an iterated Prisoner's Dilemma (Axelrod and Hamilton, 1981), in which a bird could opt to "cooperate" (return from foraging trips in a "reasonable" amount of time) or "cheat" (remain at sea longer, leaving its mate to pay a continuing cost of being food-deprived).

The risk of an overly lengthy foraging bout, and hence the cost of cheating in the Prisoner's Dilemma, is that the nest may fail due to depletion of the incubator's body reserves (Davis, 1982; Olsson, 1997; Tverra et al., 1997). In a variety of seabird species, desertion of the egg or chick occurs when the attending parent suffers a reduction in body condition, generally after a period of fasting on the nest (Davis, 1982; Erikstad et al., 1997; Monaghan et al., 1992; Weimerskirch, 1995). In a similar way, frigatebird nests fail during incubation primarily for reasons that are likely related to the incubator's body condition. In addition to incubators abandoning nests after prolonged absences by mates, other direct causes of frigatebird nest failure include the egg falling to the ground and breaking as a result of aggressive interactions between birds, and unpaired males successfully evicting incubators and taking over their nest structures. These two types of nest failure are likely to occur disproportionately often during long incubation shifts: the incubator may be weak and thus less able to fend off aggressors, or the incubator may be less willing to invest in nest defense as the bird approaches a threshold for abandonment (Chaurand and Weimerskirch, 1994). Thus, the main causes of frigatebird nest failure during incubation are likely increased by the prolonged absence of the foraging member of the pair.

In this study, I determine whether body condition or retaliation plays a role in the parental effort decisions of incubating great frigatebirds. First, to determine whether body condition has the potential to affect parental effort decisions, I test whether body mass is lost during incubation and regained during the subsequent foraging trip. Second, I test whether an incubating bird that is left on the nest for an extended period of time while its mate forages will subsequently remain at sea for a longer period of time after being relieved by its mate, a pattern that would be consistent with both body condition and retaliation. Third, I ask whether long incubation shifts are more likely to end in nest failure. Finally, I use a food supplementation experiment to test whether the long foraging trips that follow long incubation shifts are due to the

need to recover body mass or due to retaliation for the prolonged absence of an individual's mate.

METHODS

Study area and species

Frigatebirds spend most of the nonbreeding season foraging pelagically over large areas but congregate in high densities on small oceanic islands to breed. This study was conducted in a breeding colony of great frigatebirds on Tern Island (23° 45' N, 166° 17' W) in the Northwestern Hawaiian Islands. Tern Island, one of 10 small islands in the French Frigate Shoals atoll, is approximately 14 ha in size and is a breeding area for 15 species of seabirds totaling over 200,000 individuals (see Amerson, 1971 for more details). The nearest neighboring colony of great frigatebirds is 600 km away. Roughly 4,000 great frigatebirds visit Tern Island to breed, although many of these individuals are males that fail to obtain mates. There are approximately 800 active frigatebird nests on Tern Island at the peak of the breeding season. Males begin displaying in January, and eggs are laid from February through the end of May. The rate of nest failure is high: in 1998 and 1999, over half of the nests that were initiated failed during incubation (unpublished data).

Frigatebirds are sexually dimorphic, with males having sexual ornaments that females lack, including a red inflatable throat pouch, a ruff of long iridescent feathers, and a complex courtship display that is conducted in dense aggregations (Nelson, 1975). Females are generally 2% to 15% larger than males in my study population (unpublished data) and are larger than males in other populations as well (Nelson, 1975; Schreiber and Schreiber, 1988).

During the incubation period, members of a pair take turns incubating and going to sea to forage. When an incubating bird is relieved by its returning mate, it leaves the nest immediately and flies away from the island. When the bird returns to the island at the end of a foraging trip, it flies directly to the nest to relieve its mate (unpublished data). Incubating birds fast while on the nest and cannot leave until their mates return because a nest unattended for even a few minutes is destroyed. Males compete for nesting material (unpublished data) and, given the opportunity, steal the sticks that comprise a nest or take over the nest entirely and subsequently display from it; in either case, the egg is destroyed. Thus, a successful breeding attempt requires coordination of incubation shifts. If an incubating individual departs the nest prior to the return of its mate, the breeding attempt fails.

On Tern Island, the incubation period of great frigatebirds lasts 57 days, with incubation shifts of on average 4 days (range 1–23). Females typically incubate for longer periods than do males; at nests that survived the entire incubation period, females incubated for more days than did their mates in both 1998 (mean difference = 10.9 ± 5.28 days; paired $t = 9.49$, $df = 20$, $p < .001$) and 1999 (mean difference = 6.4 ± 4.18 days; paired $t = 7.17$, $df = 21$, $p < .001$).

Mass loss of incubating males

I measured the mass loss of 10 male frigatebirds over the course of an incubation shift. Mass loss data could be collected only from males because females frequently abandon their nests if handled during the incubation period. Beginning with either the first (for males that arrived that morning) or the second day of a shift (for males that arrived on the previous afternoon), males were weighed every second day until the end of that shift, for a median of three times each (range 2–4). Six of the 10 males were then weighed a final time after returning from their at-sea foraging bout (i.e., at the start of their next incubation shift). Birds were weighed between 1430

and 1730 HST, and all measurements were made between 19 March and 13 April 1999. For all birds, the start of the shift in which the bird was weighed occurred during the first half of the 57-day incubation period (median days postlaying = 18, range 1–27). Because the structural size of a bird does not change over a short time span, and because this study asks questions about changes in condition within rather than between individuals, body mass is a good index of body condition in this study (see Chaurand and Weimerskirch, 1994; Weimerskirch, 1995; Weimerskirch et al., 1997).

Relationship between time incubating and time foraging

Nests were monitored from the start of the breeding season in late January through mid-July in 1998 and through the beginning of May in 1999. The lengths of incubation shifts and foraging bouts were determined by checking nests twice per day (0800 and 1730). For each nest at which I knew the date of egg-laying ($n = 344$), I randomly selected the male or the female for analysis. If there were at least two complete incubation shifts and foraging trips for the chosen individual (i.e., the nesting attempt did not fail during that period), I calculated the slope of the linear regression of foraging shift length as a function of previous incubation shift length, using data from that single nest. After performing this analysis individually for each nest ($n = 153$ nests), I used an ANOVA to test whether variation in slopes was accounted for by sex, year, or the interaction. Because none of these effects was significant (sex: $F_{1,149} = 1.45$, $p = .23$; year: $F_{1,149} = 2.04$, $p = .16$; sex \times year: $F_{1,149} = 0.19$, $p = .66$), I combined both sexes and both years and used a t test to determine if the mean slope was significantly different from zero.

Foraging excursion length and nest success

To examine the extent to which prolonged foraging excursions contribute to nest failure (Olsson, 1997), I compared the lengths of incubation shifts that ended in failure to those from nests at which the egg eventually hatched. I measured the lengths of all incubation shifts from 21 nests (281 shifts) in 1998 and 22 nests (257 shifts) in 1999 that were monitored from egg-laying through hatching. I used the lengths of these shifts to generate an expected distribution of shift lengths against which I compared the lengths of incubation shifts that ended in failure (one shift from each of 131 failed nests in 1998 and 140 failed nests in 1999). Because shift length varied by year and by sex, I used two-sample Kolmogorov-Smirnov tests to make four separate comparisons (i.e., for each combination of sex and year) of the distribution of the lengths of failed shifts versus the distribution of all shift lengths from nests that hatched.

Food supplementation experiment

A positive relationship between foraging bout duration and incubation shift duration is consistent with both the body condition hypothesis and the retaliation hypothesis. To distinguish between body condition and retaliation as primary determinants of parental effort decisions in frigatebirds, I conducted a food supplementation experiment from 26 February through 3 April 1999. I provided food to incubating birds that were in the midst of a long incubation shift. In 1998, the mean (\pm SD) length of incubation shifts not ending in nest failure was 4.2 ± 1.53 days ($n = 534$ shifts at 63 nests). For the food supplementation experiment, I defined "long" incubation shifts as those lasting at least 6 days. The length of the incubation shift and the subsequent foraging shift were determined by twice-daily nest checks.

The experiment was restricted to nests with known egg-laying dates (median lay date = 3 March 1999, range 10 February–19 March). I randomly assigned nests at their first long

incubation shift to control or fed treatments; only one parent was used at each nest. Beginning on day 6 of that incubation shift, birds in the fed treatment were offered fish *ad lib* each day, until relieved by their mates. The fish used were Pacific sardines (*Sardinops sagax*, Fam. Clupeidae), with an average mass of 69.5 g (± 10.2 SD, $n = 104$). The diet of great frigatebirds in the Northwestern Hawaiian Islands is approximately 85% fish, the majority of which are flying fishes (Family Exocoetidae), a group of species roughly the size of Pacific sardines (Harrison et al., 1983). Each sardine was weighed to the nearest gram, and birds were fed by clipping the fish on a 0.7 m length of monofilament line at the end of a 3 m pole. I sat on the ground approximately 3 m from the nest and dangled the fish in front of the incubating bird. The bird grabbed the fish, pulled it from the clip, and swallowed it headfirst (as they do with natural fish prey). Fish were offered in this manner until the bird was no longer interested.

The body condition hypothesis predicts that the posttreatment foraging excursion of fed birds would be of shorter duration than that of unfed birds, whereas the retaliation hypothesis predicts that the trips would be of equal duration (i.e., no effect of treatment). In exploratory regression analyses, there was no consistent effect of incubation shift length on forage duration within this set of long-incubation-shift birds, so incubation shift length was not used as a covariate in the final analysis. I used a two-way fixed effects ANOVA, with foraging duration as the dependent variable and with treatment (control versus fed), sex, and the treatment \times sex interaction as predictor variables, to test the body condition and retaliation hypotheses.

The body condition hypothesis would be further supported if, among experimentally fed birds, individuals that ate more fish returned from the subsequent foraging excursion sooner than did individuals that ate less fish. I thus conducted two regression analyses, using total mass of sardines, and total mass of sardines divided by length of the incubation shift (i.e., mass of fish per day) as predictor variables. In initial analyses, I tested whether posttreatment foraging duration was related to sex, amount of fish, or the interaction; because the interaction term was significant ($t = -3.33$, $p = .004$), I subsequently performed separate tests for males and females.

A further test of the retaliation hypothesis can be made by analysis of the posttreatment foraging trips of fed birds. If, in addition to the absence of treatment effect in the ANOVA, there was a positive relationship between the duration of the posttreatment foraging excursion and the duration of the previous incubation shift, this would indicate that individuals are scaling their retaliation (i.e., adjusting the amount of time that they stay at sea).

Finally, it is possible that a weak effect of retaliation on parental care decisions could be masked by a strong effect of body condition. In this case, there would be an overall treatment effect in the ANOVA (i.e., fed birds would return from foraging sooner than controls), but among fed birds there would be a positive relationship between duration of the incubation shift during which they were fed and duration of the subsequent foraging trip. Such a relationship would indicate a weak retaliatory response because the large effect of body condition on foraging trip duration would have been removed by the experimental feedings. Thus, for fed birds I regressed foraging trip duration on incubation shift duration, examining males and females separately.

Critical assumptions were met for all statistical tests. Analyses were conducted with SPSS (SPSS Inc., 1995) and R (Ihaka and Gentleman, 1996).

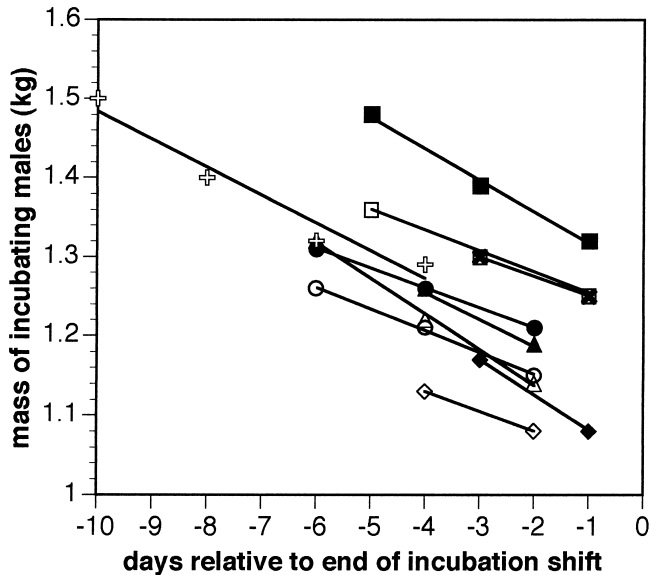


Figure 1
Mass loss by 10 male great frigatebirds measured at two-day intervals over a single incubation shift in 1999. Median length of these 10 incubation shifts was 5.5 days, and average daily mass loss was 33 ± 8.2 g (= daily loss of 2.5% of starting body mass). Each line depicts the least-squares regression for an individual.

RESULTS

Mass loss of incubating males

The median length of these incubation shifts was 5.5 days (range 3–10), and average mass loss (\pm SD) for the 10 males was 33 ± 8.2 g day⁻¹ (Figure 1). Mean mass of the males at the beginning of the incubation shift was 1310 ± 120 g, so this mass loss represents an average daily loss of 2.54% of a male's body mass relative to the first time he was weighed at the start of the incubation shift.

The mass of six males weighed upon return from their foraging excursion was not different from their mass at the start of the previous incubation shift (average difference in mass 1.7 ± 64.3 g; paired *t* test: $t = -0.06$, *df* = 5, $p = .95$). Thus, mass loss over an incubation shift was on average balanced by mass gain during the subsequent foraging bout.

Relationship between time incubating and time foraging

Individual regressions of foraging trip duration versus incubation shift duration were calculated for 55 birds in 1998 (25 males, 30 females) and for 98 birds in 1999 (49 males, 49 females) and were based on a median of four incubation shifts per bird (range 2–11). The average slope was significantly greater than zero (mean slope = 0.51 ± 1.17 ; $t = 5.35$, *df* = 152, $p < .001$). Thus, duration of a foraging trip was positively related to duration of the preceding incubation shift, as predicted by both the body condition hypothesis and the retaliation hypothesis.

Consequences of long foraging bouts on nest success

The distribution of shift lengths ending in nest failure was significantly different from the distribution of shift lengths at nests that survived to hatch. Significant differences were found among females in 1998 ($n_{\text{hatch}} = 141$ shifts, $n_{\text{fail}} = 79$ shifts, K-S D = 0.404, $p < .0001$), females in 1999 ($n_{\text{hatch}} = 130$ shifts, $n_{\text{fail}} = 82$ shifts, K-S D = 0.213, $p = .021$), and males in 1999 ($n_{\text{hatch}} = 127$ shifts, $n_{\text{fail}} = 58$ shifts, K-S D = 0.220, $p = .042$); the difference among males in 1998 was nearly significant ($n_{\text{hatch}} = 137$ shifts, $n_{\text{fail}} = 52$ shifts, K-S D = 0.219, p

= 0.055). Within each combination of sex and year, the main difference in shift length distributions was the longer duration of the shifts that ended in failure (Figure 2).

Food supplementation experiment

The food supplementation experiment involved 26 control birds (10 males, 16 females) and 20 fed birds (7 males, 13 females). Birds in the fed treatment ate an average of 5.2 ± 1.67 fish and an average total fish mass of 361.6 ± 115.6 g. Fed and control birds did not differ in the length of the incubation shift during which the treatment was applied (Figure 3a); in a two-way ANOVA of incubation shift length, using treatment and sex as factors, there was no effect of treatment ($F_{1,42} = 0.01$, $p = .927$) or interaction ($F_{1,42} = 0.20$, $p = .653$), but males incubated for shorter shifts than did females ($F_{1,42} = 14.79$, $p < .001$).

The duration of the subsequent foraging excursion, however, was significantly shorter for fed birds than for control birds (mean for fed birds = 5.35 days, mean for control birds = 7.15 days; ANOVA, $F_{1,42} = 14.09$, $p = 0.001$; Figure 3b). Foraging trips of males were longer than those of females (ANOVA, $F_{1,42} = 6.60$, $p = 0.014$), and there was no interaction between treatment and sex ($F_{1,42} = 2.63$, $p = .112$). Because the interaction effect approached significance and because an interaction is suggested by Figure 3b, I performed a Tukey pairwise comparison. The duration of the posttreatment foraging excursions differed between control females and fed females (difference of 2.27 days [95% CI: 0.91–3.63]) but not between control males and fed males (0.90 days [-0.90–2.70]). This result indicates that for females there was an effect of feeding treatment on length of the subsequent foraging excursion, supporting the body condition hypothesis for females.

Among fed females, but not among fed males, the duration of the posttreatment foraging excursion was negatively related to amount of fish eaten during incubation (Figure 4a,b). This was true whether based on total mass of fish eaten (males: $B = 0.010$, $t = 0.578$, $p = .589$, $r^2 = .062$; females: $B = -0.013$, $t = -3.42$, $p = .0057$, $r^2 = .516$) or on mass of fish adjusted to the duration of the incubation shift (males: $B = 0.059$, $t = 0.29$, $p = .782$, $r^2 = .017$; females: $B = -0.202$, $t = -3.10$, $p = .010$, $r^2 = .418$). The smaller sample size of males relative to females resulted in low power to detect a relationship between foraging trip duration and amount fed (power = 0.11 to detect a regression of same slope as found for females; Neter et al., 1989), but data from this sample of males are not suggestive of such a relationship (Figure 4).

Although the feeding experiment supported the body condition hypothesis for female frigatebirds, there remains the possibility, particularly for males, that some level of retaliation was displayed by experimentally fed birds: if foraging bout length was positively related to incubation shift length for fed birds (regardless of a treatment effect in the ANOVA), this would provide evidence of retaliatory behavior. However, results of the regression of foraging bout length on incubation shift length for fed birds indicate that there was no relationship between these two variables for fed males ($B = 1.84$, $t = 1.06$, $p = .34$) or fed females ($B = -0.09$, $t = -0.28$, $p = .79$). Power to detect a slope of 0.51 (the mean slope from all within-nest analyses of nonexperimental birds) was low for both males (power ~ 0.10) and females (power = 0.30; Neter et al., 1989). When using adjusted mass of fish eaten as an additional predictor in the model, there was still no effect of incubation shift length on posttreatment foraging trip duration for males ($B = 1.861$, $t = 0.972$, $p = .386$) or females ($B = -0.230$, $t = -0.927$, $p = .376$).

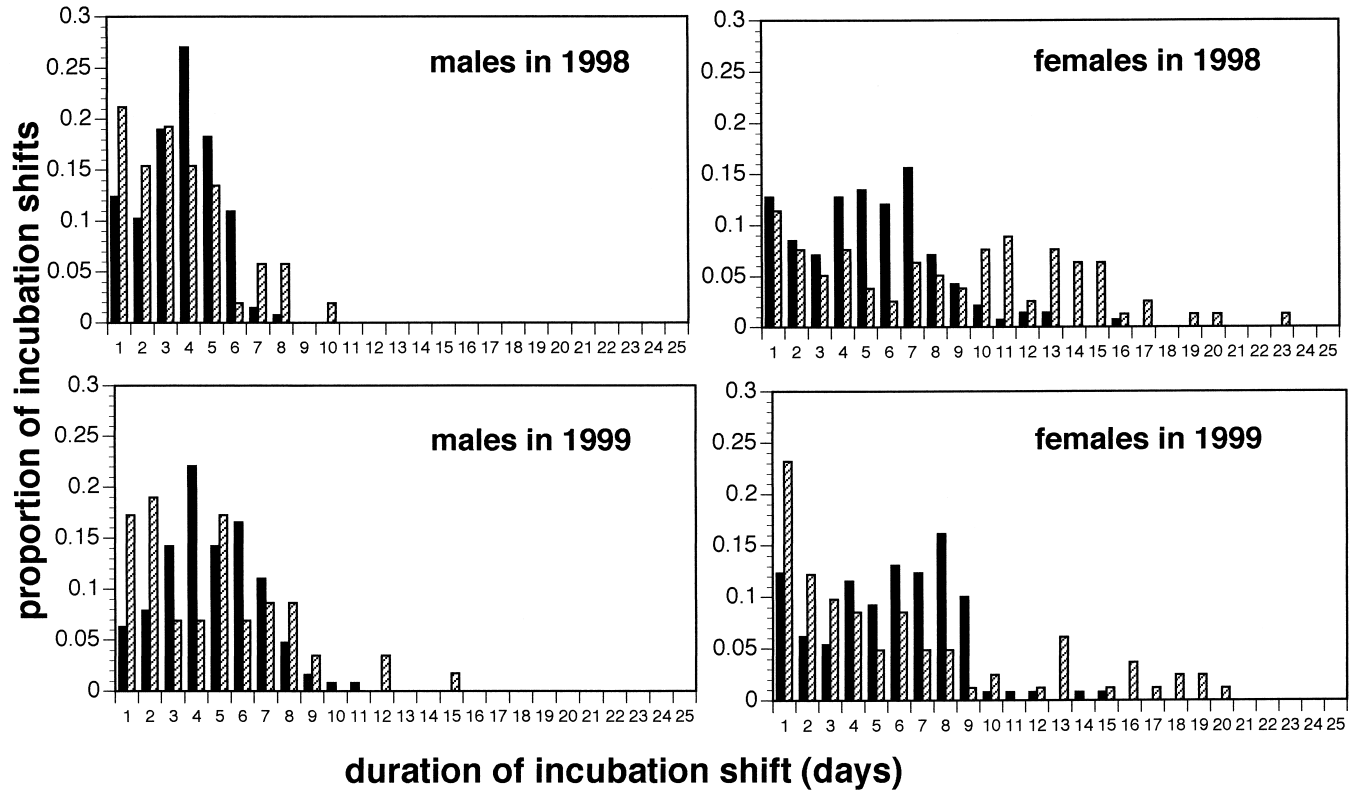


Figure 2

Frequency distribution of incubation shift lengths for (a) males in 1998, (b) males in 1999, (c) females in 1998, and (d) females in 1999. The lengths of shifts that culminated in nest failure (hatched bars) were compared against an expected distribution of shift lengths (black bars) generated by measuring all incubation shifts at nests that survived to hatch. Significant differences were detected for all comparisons except 1998 males (see text for details).

DISCUSSION

The results of this study indicate that body condition affects the parental effort decisions of incubating great frigatebirds. First, individuals lost mass while incubating and then regained this mass on the subsequent foraging excursion, indicating that body condition has the potential to affect parental effort decisions. As predicted by both the body condition hypothesis and the retaliation hypothesis, long incubation shifts were followed by long foraging excursions. These long shifts were more likely to culminate in nest failure, indicating a cost to prolonged foraging excursions. The feeding experiment showed that, among frigatebirds involved in long incubation shifts, birds that were experimentally fed returned from their subsequent foraging trip sooner than did birds that were not fed. Thus, the positive relationship between incubation shift duration and foraging trip duration is largely driven by the depleted condition, or the need to recover body mass, of the bird that goes to forage. If retaliation were the main determinant of parental effort decisions, the food supplementation treatment should not have produced an effect on forage trip duration. Birds that had been left on the nest for a long time by their mates would retaliate by going on a long “foraging” trip, even though I had fed them during their long incubation shift.

Despite this overall effect, several lines of evidence suggest that males and females differ in the extent to which their parental effort decisions are governed by the need to recover body mass rather than by retaliation. First, pairwise comparisons of posttreatment trip duration detected a difference only between fed and control females; fed and control males did not differ. Second, for experimentally fed females, there was

a negative relationship between the duration of the posttreatment foraging excursion and the amount of fish consumed during incubation. This further indicates that body condition is a main factor determining female foraging trip duration.

There was no clear evidence for an effect of the feeding treatment on the subsequent foraging excursion of males. Furthermore, among fed males there was no relationship between duration of the posttreatment foraging excursion and the amount of fish that males consumed during the experiment, suggesting that retaliation, rather than body condition, may influence the parental effort decisions of males.

Males and females also differed in the extent of differences in the lengths of successful incubation shifts versus shifts ending in nest failure: for females, successful shifts were substantially shorter than shifts that ended in nest failure, but this difference was less distinct for males. This pattern, coupled with the overall tendency for males’ incubation shifts to be shorter than females’, suggests that males are either unwilling or unable to remain on the nest for extended periods of time. Unwillingness would be consistent with retaliation, whereas inability would be consistent with males’ greater susceptibility to depletion of body reserves.

In considering these differences between male and female great frigatebirds, it may be helpful to review other sex differences in this species. Although parental care is quite balanced between the sexes relative to most species of birds, males spend less time incubating and more time foraging than do females, and females care for fledglings for 1–2 months longer than do males. (But note that this difference is much less pronounced than in magnificent frigatebirds, *F. magnificens*, where males desert their mates very early in the chick-

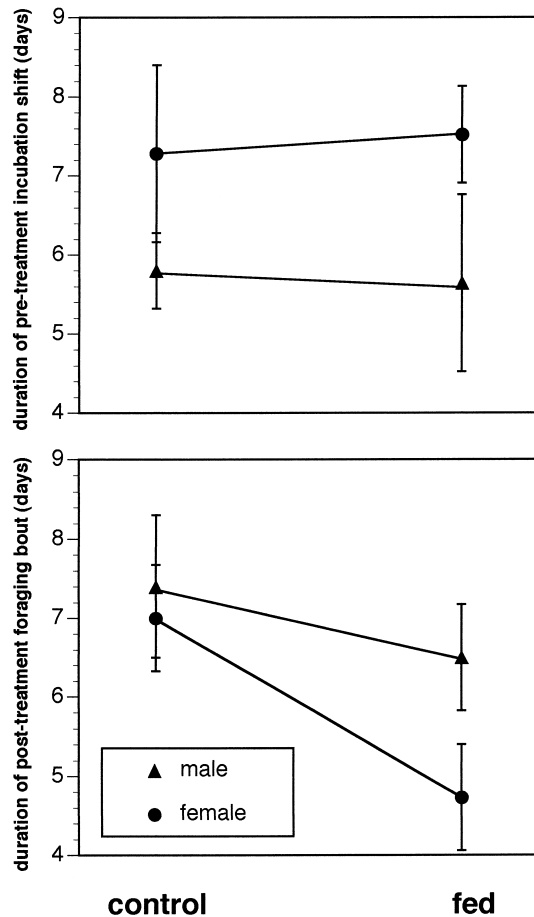


Figure 3

(a) Mean (\pm 95% CI) duration of incubation shifts during which treatments were applied. Males incubated for shorter shifts than did females (ANOVA, $F_{1,42} = 14.79$, $p < 0.001$); as expected, fed birds and control birds did not differ ($F_{1,42} = 0.01$, $p = .927$), and there was no interaction ($F_{1,42} = 0.20$, $p = .653$). (b) Mean duration of foraging trips immediately following the incubation shift during which treatment was applied. Fed birds ate an average of 362 g of fish while incubating, and control birds were not fed. Fed birds returned from the subsequent foraging bout significantly sooner than did control birds (ANOVA: $F_{1,42} = 14.09$, $p = 0.001$), and females returned sooner than did males ($F_{1,42} = 6.60$, $p = 0.014$). The interaction was not significant ($F_{1,42} = 2.63$, $p = .112$), but Tukey pairwise comparisons detected differences only between control females and fed females.

rearing period; Osorno, 1999.) Males are smaller-bodied than females, thus raising the possibility that they may lose a larger percentage of overall body mass during an incubation shift than do females, which could require males to spend relatively longer periods foraging between incubation shifts than do females. Sex differences in parental effort have also been shown in the wandering albatross (*Diomedea exulans*), a seabird species with biparental care and long-term pair bonds. In the wandering albatross, males and females differ in the extent and pattern of parental effort due to differences in their use of pelagic versus near-shore foraging areas (Weimerskirch, 1995; Weimerskirch et al., 1997). Little is known about the foraging range of frigatebirds, but the differences in male and female morphometrics (Schreiber and Schreiber, 1988) might select for differences in foraging, which could, in turn, influence the factors that govern parental effort. One final potential explanation for the differences in parental effort between male and female frigatebirds is based on paternity assurance.

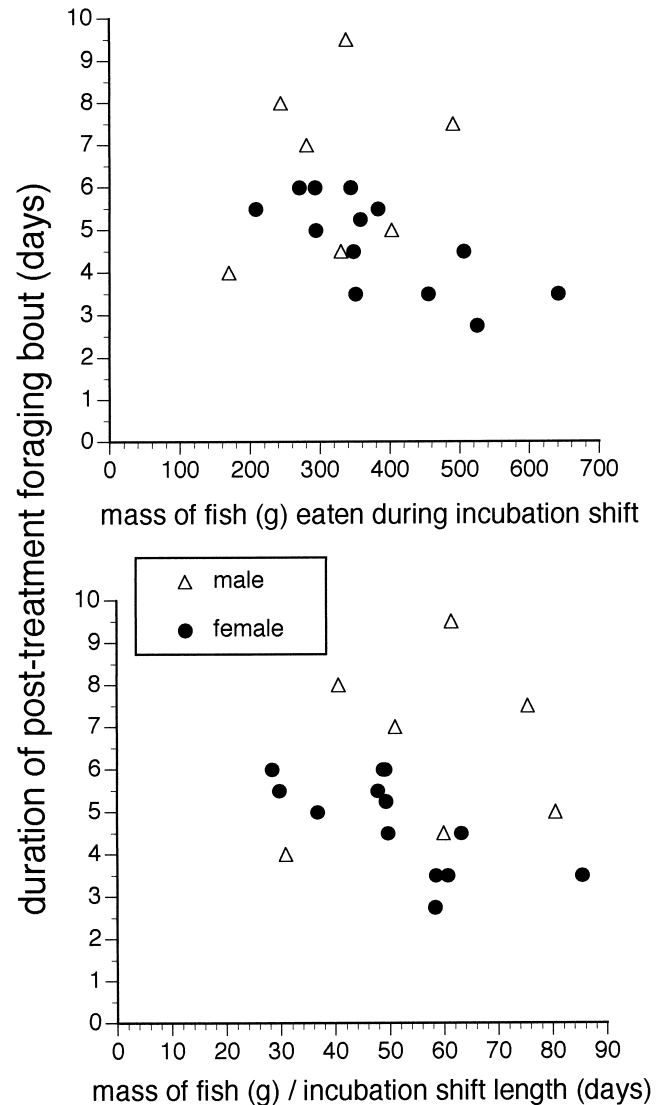


Figure 4

Relationship between duration of posttreatment foraging trip and amount of fish eaten during the experimental incubation shift. Data are only for birds that were experimentally fed, and males and females are shown separately. Regression was significant for females but not for males. (a) Predictor variable is total mass of fish eaten during incubation. Regression was significant for females but not for males. (b) Predictor variable is total mass of fish divided by length of incubation shift during which birds were fed. Regression was significant for females but not for males.

Because males of some species have been shown to reduce their parental care in response to low likelihood of paternity (Johnson and Burley, 1998), male frigatebirds might be retaliatory in their parental effort decisions due to uncertainty of paternity. However, paternity analysis of family groups indicates that the frequency of extra-pair fertilizations is extremely low in my study population (Dearborn D, Anders A, Parker P, manuscript in review).

Previous studies of factors influencing parental effort decisions have focused on short-lived species or on long-lived species with long-term pair bonds. In such species, body condition has been shown to affect parental effort decisions (Chastel et al., 1995; Erikstad et al., 1997; Hegyi and Sasvari, 1998; Wright and Cuthill, 1989). However, perhaps due to limited life span (and thus limited breeding opportunities) or to the

benefits of maintaining pair bonds, response in such species to low parental effort by the mate is compensation rather than retaliation (Saino and Møller, 1995; Sasvari, 1986; Tveraa et al., 1997). Results of this study indicate that, as with these other species, parental effort decisions of great frigatebirds are affected by body condition. However, because great frigatebirds are long-lived and have short-term pair bonds, we might expect them to exhibit some degree of retaliation when faced with low parental effort by the mate. This study did not find strong evidence of such retaliation in frigatebirds, although further study may strengthen the evidence that males of this species do exhibit some degree of retaliation.

Angela Anders helped plan and conduct the fieldwork and made many useful suggestions on the manuscript. I thank Patty Parker and Mike Ryan for additional advice and support. Funding was supplied by an Ohio State University Postdoctoral Fellowship and by the American Philosophical Society. Permits and logistical support were provided by the personnel of the Hawaiian Islands National Wildlife Refuge, especially Beth Flint, Brian Allen, and Dominique Aycock. Pete Hurd and two anonymous reviewers made helpful comments on the manuscript.

REFERENCES

- Amerson AB Jr, 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. *Atoll Res Bull* 150:1–383.
- Axelrod R, Hamilton WD, 1981. The evolution of cooperation. *Science* 211:1390–1396.
- Cézilly F, Nager RG, 1996. Age and breeding performance in monogamous birds: the influence of pair stability. *Trends Ecol Evol* 11:27.
- Chastel O, Weimerskirch H, Jouventin P, 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76:2240–2246.
- Chaurand T, Weimerskirch H, 1994. Incubation routine, body mass regulation, and egg neglect in the blue petrel, *Halbaena caerulea*. *Ibis* 136:285–290.
- Choudhury S, 1995. Divorce in birds: a review of the hypotheses. *Anim Behav* 50:413–429.
- Davis L, 1982. Timing of nest relief and its effect on breeding success in Adelie penguins (*Pygoscelis adeliae*). *Condor* 84:178–183.
- Erikstad KE, Asheim M, Fauchald P, Dahlhaug L, Tveraa T, 1997. Adjustment of parental effort in the puffin: the roles of adult body condition and chick size. *Behav Ecol Sociobiol* 40:95–100.
- Harrison CS, Hida TS, Seki MP, 1983. Hawaiian seabird feeding ecology. *Wildl Monogr* 85:1–71.
- Hegy Z, Sasvari L, 1998. Parental condition and breeding effort in waders. *J Anim Ecol* 67:41–53.
- Houston AI, Davies NB, 1985. The evolution of cooperation and life history in the dunnoek, *Prunella modularis*. In: *Behavioural ecology: ecological consequences of adaptive behaviour* (Sibly RM, Smith RH, eds). Oxford: Blackwell Scientific; 471–487.
- Ihaka R, Gentleman R, 1996. R: a language for data analysis and graphics. *J Comp Graph Stat* 5:299–314.
- Johnson K, Burley NT, 1998. Mating tactics and mating systems of birds. In: *Avian reproductive tactics: male and female perspectives* (Parker PG, Burley NT, eds). Washington, DC: American Ornithologists' Union; 21–60.
- Markman S, Yom-Tov Y, Wright J, 1995. Male parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. *Anim Behav* 50:655–669.
- Monaghan P, Uttley JD, Burns MD, 1992. Effect of changes in food availability on reproductive effort in Arctic terns *Sterna paradisaea*. *Ardea* 80:71–81.
- Nelson JB, 1975. The breeding biology of frigatebirds: a comparative review. *Living Bird* 14:113–155.
- Neter J, Wasserman W, Kutner MH, 1989. *Applied linear regression models*. Homewood, IL: Richard D. Irwin.
- Olsson O, 1997. Clutch abandonment: a state-dependent decision in king penguins. *J Avian Biol* 28:264–267.
- Osorno J-L, 1999. Offspring desertion in the magnificent frigatebird: are males facing a trade-off between current and future reproduction? *J Avian Biol* 30:335–341.
- Prince PA, Rothery P, Croxall JP, Wood AG, 1994. Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 136:50–71.
- Reville BJ, 1988. Effects of spacing and synchrony on breeding success in the great frigatebird (*Fregata minor*). *Auk* 105:252–259.
- Saino N, Møller AP, 1995. Testosterone-induced depression of male parental behavior in the barn swallow: female compensation and effects on seasonal fitness. *Behav Ecol Sociobiol* 36:151–157.
- Sasvari L, 1986. Reproductive effort of widowed birds. *J Anim Ecol* 55:553–564.
- Schreiber EA, Schreiber RW, 1988. Great frigatebird size dimorphism on two Central Pacific atolls. *Condor* 90:90–99.
- SPSS Inc, 1995. *SPSS for PowerMac*, 6.1.1. Chicago, IL: SPSS.
- Tveraa T, Lorentsen S-H, Saether B-E, 1997. Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (*Thalassoica antarctica*). *Behav Ecol* 8:465–469.
- Weimerskirch H, 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* 102:37–43.
- Weimerskirch H, Chastel O, Ackermann L, 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav Ecol Sociobiol* 36:11–16.
- Weimerskirch H, Cherel Y, Cuenot-Chaillet F, Ridoux V, 1997. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* 78:2051–2063.
- Williams GC, 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *Am Nat* 100:687–690.
- Wright J, Cuthill I, 1989. Manipulation of sex differences in parental care. *Behav Ecol Sociobiol* 25:171–182.