ANIMAL BEHAVIOUR, 2004, **68**, 337–342
doi:10.1016/j.anbehav.2003.06.027

Sexual conflict and parental care in magnificent frigatebirds: full compensation by deserted females

JOSÉ LUIS OSORNO[*,1] **& TAMÁS SZÉKELY**[†]
*Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México
†Department of Biology & Biochemistry, University of Bath

*(Received 21 May 2002; initial acceptance 13 January 2003;
final acceptance 26 June 2003; MS. number: A9362R)*

Parental care is a cooperative venture between a male and a female in many socially monogamous birds. Care is costly, and thus, sexual conflict arises between the parents about how much effort they should invest into rearing their young. The sexual conflict over care is most apparent when one parent abandons the brood before the offspring are independent. The deserted parent has three options: (1) desert the brood because a single parent is unable to raise the young on its own; (2) continue care provision at the same level as during biparental care, and thus do not compensate for the absence of mate; or (3) increase care and compensate partially or totally. We investigated these options in the magnificent frigatebird, *Fregata magnificens*, a species in which the male deserts his mate and brood before the chick is independent. During biparental care, females fed the chick more often than the males. After their mate deserted, the females nearly doubled their feeding rate and thus, fully compensated for the lost care. Consistent with these observations, growth rates of chicks provided with biparental and female-only care did not differ. These results support recent theoretical models of parental care, and suggest that females may withhold care during biparental care to manoeuvre their mates into prolonged care provision. A female only provides at her full capacity once her mate has deserted.

Sexual conflict between males and females is expected to influence the patterns of parental care, because if care is costly, each parent may do better by shunting the care to its mate (Trivers 1972). The solution to sexual conflict over care (i.e. postzygotic sexual conflict, Royle et al. 2002) depends on the costs and benefits of care for each parent (Carlisle 1982; Kelly & Kennedy 1993), and the process of decision making (Houston & McNamara 1999). These costs and/or benefits may be influenced by the behaviour of a parent's mate (e.g. whether the mate is willing to compensate for the lost care: Bart & Tornes 1989; Wright & Cuthill 1989; Slagsvold & Lifjeld 1990; Markman et al. 1995; Winkler & Allen 1995), and by the behaviour of other animals in the population, for instance, via remating opportunities for the deserting animal (Balshine-Earn & Earn 1998; Pilastro et al. 2001; Bennett & Owens 2002). One solution to sexual conflict is offspring desertion whereby one parent terminates care before the offspring reach independence (Székely et al. 1996). Parental decisions and offspring desertion are typically investigated using game-theoretic models (Maynard Smith 1982; Hammerstein & Parker 1987; Houston & McNamara 1999; Székely et al. 2000): the parents may decide once for each batch of offspring whether to provide care or desert (Maynard Smith 1977; Webb et al. 1999), or one (or both) parents may settle on offspring desertion through repeated interactions (McNamara et al. 1999, 2003).

The deserted parent has three options. First, a parent may terminate care to retaliate the decision of its mate, or because a single parent on its own is unable to raise the young successfully. This is costly, because desertion by both parents dooms the offspring to death in most birds and mammals (Clutton-Brock 1991; Székely et al. 1996). Second, the deserted parent may continue to provide care at the same level as before desertion, although the lower total care during uniparental care may reduce offspring survival (Ezaki 1988; Cezilly 1993; Székely & Williams 1995). Finally, the deserted parent may increase its parental effort to compensate for the lost care from its

---

Correspondence: T. Székely is at the Department of Biology & Biochemistry, University of Bath, Bath BA2 7AY, U.K. (email: t.szekely@bath.ac.uk). J. L. Osorno, Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, A. P. 70-275, México, D.F. 04510, México.

[1] *J. L. Osorno died shortly after completing this work.*

0003–3472/03/$30.00/0

mate (Gratto-Trevor 1991; Urano 1992; Sanz et al. 2000). This compensation may be partial or total, or the deserted parent may even overcompensate (McNamara et al. 2003). Because the parent works harder after desertion, the increased parental response is expected to increase adult mortality and/or reduce reproductive output in future breeding seasons (reviewed by Clutton-Brock 1991; Roff 1992).

We investigated the behavioural response of female magnificent frigatebirds, *Fregata magnificens*, to desertion by their mates. In this socially monogamous seabird, the males always desert their single offspring between the ages of 18 and 160 days, and then begin to moult (Osorno 1999). Males that desert young chicks return to the breeding colony more often than males that desert old chicks, presumably because early-deserting males have more time to complete moult (Osorno 1999). The female continues to feed the chick until the chick fledges and leaves the nest (Osorno 1996), and she may even continue to feed the fledged young. Specifically, we investigated whether female frigatebirds respond to desertion by their mate by providing the same level of parental effort during female-only care as during biparental care, or by increasing their parental effort to compensate for the lost care from their mate.

METHODS

Field Work

We studied the magnificent frigatebirds at Isla Isabel, Nayarit, Mexico (21°52′N, 105°54′W) between 20 February and 21 July 1994. We monitored 40 broods with one chick each. Monitoring began at a mean ± SE age of 40.1 ± 2.8 days. We estimated initial chick age and hatching date from a growth curve fitted to the culmen length of 13 chicks that hatched at known dates in 1991 ($r^2 = 0.935$, $P < 0.0001$; Durand 1992). The precise hatching dates of these chicks were not known, because we avoided visiting nests around the time of hatching.

We conducted focal observations of 36 nests simultaneously, from an observation tower 30–150 m away from the nests (see details in Osorno 1999). Feedings by parent(s) and chick survival were recorded on three consecutive days every week between 0800 and 1800 hours until the chick fledged ($\overline{X} \pm$ SE age at first flight: 180.8 ± 3.3 days, $N = 25$ chicks), died ($N = 3$ chicks) or disappeared from the nest ($N = 6$ chicks). The latter chicks were probably depredated. We terminated observations on 21 July 1994 when six chicks were still in the nest (age = 129.67 ± 4.8 days). Once a week, we weighed the chicks, and measured their culmen and ulna lengths. Chicks were measured at night to minimize disturbance.

Data Processing

Desertion by the male was identified when the male did not attend the chick on four consecutive days of behavioural observation. Two males were fitted with radiotransmitters in 1999, and satellite tracking of both males confirmed that males not seen at their nest for 4 days permanently left the breeding colony (J. L. Osorno, unpublished data). Male desertion occurred in all broods, including 31 successful nests (i.e. in 25 nests in which the chick survived until fledging, and six nests in which the chick was alive and near fledging when we left the island; see above) and nine unsuccessful nests.

We calculated laying date from the estimated hatching date of the chick and by using the incubation period of 56.4 ± 1.1 days ($N = 7$ nests; Osorno 1996). We calculated chick growth in two steps. First, we fitted four types of growth curves to the culmen length (in mm) and age (in days) of all chicks together ($N = 781$ measurements). The best fit was provided by the von Bertalanffy curve ($\text{culmen} = 139.39 - (139.394 - 13.060) \times \exp(-0.015 \times \text{age})$; Pearson correlation coefficient $r = 0.955$), whereas the exponential equation ($\text{culmen} = 135.952(1 - \exp(-0.017) \times \text{age})$; $r = 0.953$), the logistic equation ($\text{culmen} = 132.864/(1 + 2.614 \times \exp(-0.026 \times \text{age}))$; $r = 0.954$) and the Gomperz equation ($\text{culmen} = 135.169 \times \exp(-\exp(0.424 - 0.021 \times \text{age}))$; $r = 0.954$) provided slightly worse fits. Second, we fitted a von Bertalanffy growth curve to each chick with at least three measurements for the period before male desertion, and another curve for the period after desertion (henceforward biparental and female-only care, respectively), and used the parameters of these growth curves in the analyses (parameters a, b and c, where a is asymptotic size (mm), b is size at maximum growth (inflection point, mm) and c is a growth rate constant (mm/day)). Thus, $\text{culmen} = a - (a - b) \times \exp(-c \times \text{age})$. Body mass and ulna length were not analysed, because they did not increase monotonically in the age range we investigated.

We sexed all fledglings using a discriminant function that was calculated from 18 fledglings of known sex (nine males and nine females from our population; Durand 1992). Adult females are about 15% larger than males and sexual size dimorphism is already apparent at the age of 150 days. The discriminating equation was $Y = -40.5 + 0.12 \times \text{culmen (in mm)} + 0.09 \times \text{ulna (in mm)}$. If $Y > 0$, then the chick was a female, whereas if $Y < 0$, then the chick was a male. For all chicks, the discriminant function gave unambiguous outcomes.

Statistical Analyses

Brood was the unit of analysis. If several data were available for a chick (e.g. male or female feeding rates: number of feeds/day), we calculated their respective means for each brood. Feeding frequency and chick age were unrelated (see Results), as would be expected for a seabird that depends on unpredictable food sources. The weight of delivered food is unrelated to chick age (least squares linear regression: $r = 0.098$, $F_{1,70} = 0.69$, $P = 0.411$; E. Tobón & J. L. Osorno, unpublished data). Feeding frequency is highly correlated with the weight of delivered food in 10 days ($r = 0.88$, $F_{1,69} = 223.7$, $P = 0.000$; E. Tobón & J. L. Osorno, unpublished data). At one nest, the male deserted before any behavioural observation was recorded; thus, the sample size for feeding rates in biparental broods was 39.

All statistical tests were two-tailed. Growth rate parameters of the von Bertalanffy model were analysed using repeated measures ANOVAs that included type of parental care (within-subject factor: biparental or female-only), sex of chick (between-subject factor) and laying date (covariate). In repeated measures ANOVAs, all pairwise interactions between factors and covariates were investigated (see Results); we report only significant interactions. We used nonparametric tests if the standard assumptions of parametric tests were violated. Coefficients of Spearman rank correlations (r_S) are given. Partial rank correlations were carried out as given by Daniel (1990). We used SPSS 10.0 and MINITAB 13.31 for data processing, and CurveExpert 1.3 for curve-fitting. We report either the median (lower quartile–upper quartile), or the mean ± SE as appropriate.

RESULTS

Biparental Broods

Females fed the chick more often than males in biparental broods (female: 0.211 (0.000–0.500) feeds/day; male: 0.125 (0.000–0.267) feeds/day; Wilcoxon matched-pairs signed-ranks test: $Z = 2.983$, $N = 39$ broods, $P < 0.003$; Fig. 1). In total, the two parents provided 0.346 (0.158–0.719) feeds/day. Feeding rate of the female was significantly correlated with the feeding rate of her mate (Spearman rank correlation: $r_S = 0.342$, $N = 39$ broods, $P = 0.033$).

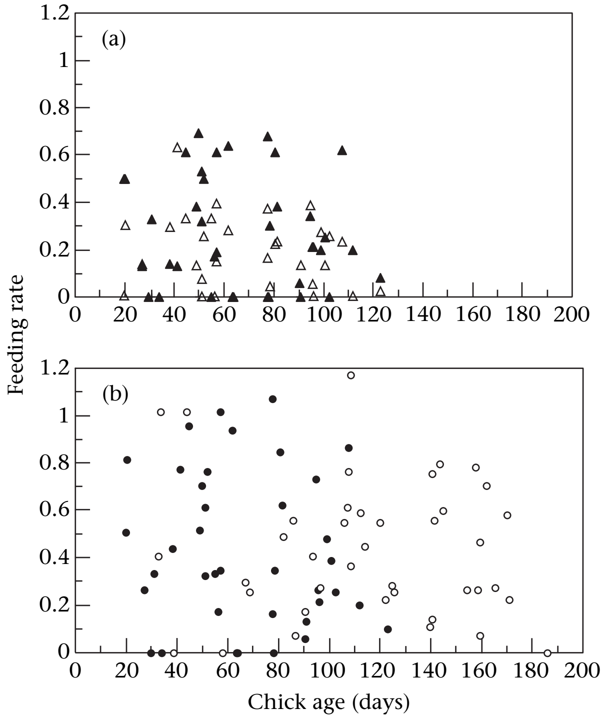

Figure 1. (a) Feeding rates (feeds/day) of females (▲) and males (△) in biparental broods, and (b) the total feeding rates in biparental (●) and uniparental broods (○) in relation to chick age in magnificent frigatebirds. The mean feeding rates for each brood are shown separately for biparental care ($N = 39$ broods) and female-only care ($N = 40$ broods) at the mean chick age.

Feeding rates were unrelated either to the age of the chick (female: $r_S = -0.099$, $N = 39$, $P = 0.550$; male: $r_S = 0.023$, $N = 39$, $P = 0.891$), or to the date of hatching (female: $r_S = 0.153$, $N = 39$, $P = 0.353$; male: $r_S = 0.121$, $N = 39$, $P = 0.461$). Finally, parental feeding rates of male chicks and female chicks did not differ (Mann–Whitney U tests: female parent: $U = 111$, $N_{\text{male chicks}} = 15$, $N_{\text{female chicks}} = 16$, $P = 0.740$; male parent: $U = 115.5$, $P = 0.861$).

Female-only Broods

After male desertion, the feeding rate of deserted females increased to 0.400 (0.228–0.583 feeds/day; Wilcoxon matched-pairs signed-ranks test: $Z = 3.147$, $N = 39$ broods, $P = 0.002$; Fig. 2). Female feeding rates in female-only broods did not differ from the total feeding rates in biparental broods ($Z = 0.015$, $N = 39$ broods, $P = 0.988$; Figs 1b, 2).

The response in female feeding behaviour to male desertion may be confounded by brood age and hatching date. Old chicks may need more frequent provisioning than young ones, and/or broods hatched late in the season may be provided more often than broods hatched early in the season, for instance, if the abundance of food increases over the season. However, brood age and hatching date are unlikely to confound our results. First, feeding rates were unrelated to brood age both in biparental broods (see above) and in female-only broods ($r_S = -0.400$, $N = 40$, $P = 0.806$). The relationships between feeding rates and brood age remained nonsignificant when controlling for hatching date and chick sex by partial rank correlation (all tests: NS). Second, feeding rates were unrelated to hatching date both in biparental

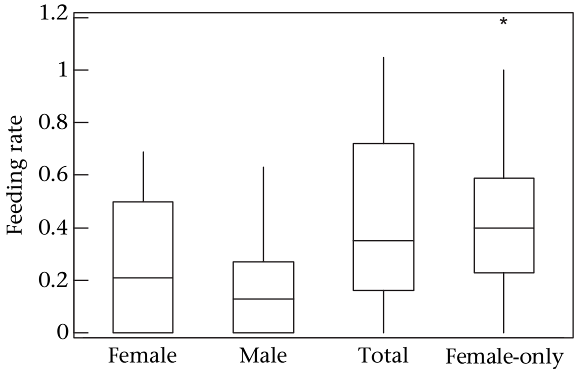

Figure 2. Boxplots of the feeding rates of females and males in biparental broods, the total feeding rates in biparental broods, and the female feeding rate in female-only broods (from left to right, number of broods 39, 39, 39, 40, see Methods). The line is drawn across the median; the bottom and the top of the box are lower quartiles (Q_1) and upper quartiles (Q_3), respectively. The whiskers extend from Q_1 and Q_3 to the lowest and highest observation, respectively, within the range defined by $Q_1 - 1.5\times(Q_3 - Q_1)$ and $Q_3 + 1.5\times(Q_3 - Q_1)$. The asterisk indicates an outlier outside the upper whiskers. The mean feeding rates were used for each brood.

Table 1. Parameters of culmen growth in chicks of magnificent frigatebird (see Methods)

	Biparental broods $\overline{X}\pm$SE	Female-only broods $\overline{X}\pm$SE	Type of care $F_{1,24}$ (*P*)*	Chick sex $F_{1,24}$ (*P*)*	Laying date $F_{1,24}$ (*P*)*
Parameter *a*	142.177±7.441	137.125±2.009	2.602 (0.120)	10.604 (0.003)	8.677 (0.007)
Parameter *b*	12.633±0.352	13.039±0.027	0.133 (0.718)	0.056 (0.815)	0.040 (0.842)
Parameter *c*	0.0179±0.001	0.0168±0.0006	1.831 (0.189)†	9.993 (0.004)†	7.738 (0.010)

Parameters: *a* = asymptotic size (mm); *b* = size at maximum growth (inflection point, mm); *c* = growth rate constant.

*Repeated measures ANOVA with type of care (within-subject factor), chick sex (between-subject factor) and egg-laying date (covariate).

†The interaction between type of care and chick sex was significant ($F_{1,24} = 5.186$, $P = 0.032$). This interaction was no longer significant in the multivariate repeated measures ANOVA (see Results, $F_{3,22} = 1.906$, $P = 0.158$).

broods (see above) and in female-only broods ($r_S = 0.264$, $N = 40$, $P = 0.099$). These relationships remained nonsignificant when controlling for brood age and chick sex by partial rank correlation (all tests: NS).

Growth Rates of Chicks

Univariate repeated measures ANOVAs showed that growth rates of biparental broods and female-only broods did not differ (Table 1). However, chicks hatched later in the season attained longer culmen (parameter *a*, Table 1), and they grew faster as well (parameter *c*, Table 1). In addition, growth rates of male and female chicks differed in that females attained longer culmen than males (Fig. 3, Table 1), and females grew faster (Table 1).

These results were confirmed by a multivariate repeated measures ANOVA in which all growth parameters (*a*, *b* and *c*) were the response variables. Growth rates of biparental care and female-only care broods did not differ ($F_{3,22} = 0.818$, $P = 0.498$), whereas both laying date and chick sex remained significantly related to growth parameters (laying date: $F_{3,22} = 3.153$, $P = 0.045$; sex: $F_{3,22} = 4.060$, $P = 0.019$).

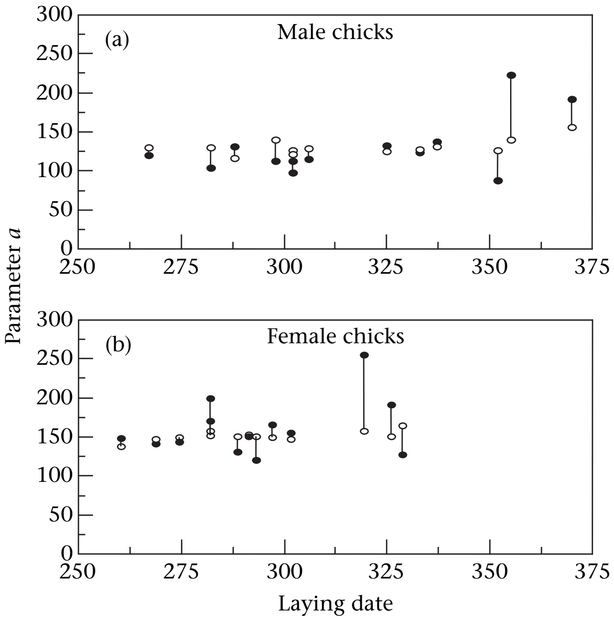

Figure 3. Culmen growth rates of (a) male and (b) female magnificent frigatebird chicks (see Methods). A von Bertalanffy growth model was fitted to each chick separately during biparental care (●) and female-only care (○). Growth rates during biparental and female-only care are connected for each chick. Laying date corresponds to the Julian date (1 January = day 1). Note that some eggs were laid in January of the following year (365 + *X* days).

DISCUSSION

Our study produced two main results. First, female frigatebirds fed the chick more often than did males. Sex differences in food deliveries also occur in other seabirds such as skuas, *Catharacta skua* and *Stercorarius parasiticus* (Caldow & Furness 2000), and the albatross *Diomedea melanophris* (Weimerskirch et al. 1996). Female skuas are larger than males by about 15% (Nelson 1975; Osorno 1996), and this reversed size dimorphism could be associated with superior female feeding ability. Also, female frigatebirds carry more food in their guts than males (Calixto & Osorno 2000) and females deliver 13% more food to their chick than males (Wilcoxon test matched-pairs signed-ranks test: $Z = -1.985$, $N = 30$, $P = 0.047$; E. Tobón & J. L. Osorno, unpublished data). However, parental roles of males and females do not differ in other sexually dimorphic seabirds such as the blue-footed booby, *Sula nebouxii* (Guerra & Drummond 1995).

Second, we also found that females did not feed the chick at their maximum level before their mates deserted, because they substantially increased their feeding rates after their mates deserted. Females fully compensated, because neither the total feeding rates nor the growth rates of chicks differed between biparental care and female-only care broods. Although chick growth rates increased over the breeding season, and female chicks grew faster than males, the growth rates of biparental and female-only chicks remained not significantly different when we statistically controlled for laying date and sex of the chick. These results are consistent with a recent field experiment, in which male frigatebirds were experimentally removed from the nest when the chick was 37 ± 2.5 days old, and the females increased their feeding effort (J. L. Osorno, unpublished data).

There are two potential explanations for the full compensation by females. First, food abundance may increase over the brood-rearing period, and thus, the high feeding rates in female-only broods may simply reflect high foraging success. This explanation is unlikely because feeding rates were not related to brood age or laying date. Also, up to 80% of the diet of the magnificent frigatebirds in our population comes from fish discarded by shrimp fishermen (Calixto & Osorno 2000), and the volume of shrimp fishery actually declines from February to July (unpublished annual reports of Mexican Fish Service for 1994–1998). The fact that chick growth increased over the breeding season may be due to the different quality of early versus late breeders (i.e. late breeders are perhaps more experienced or they may have better body condition), to the lower metabolic costs late in the breeding season due to increased ambient temperatures, or to a greater amount of food provided by the single female with the same feeding regime.

Alternatively, our results are in line with the predictions of two recent models of sexual conflict and parental care (Barta et al. 2002; McNamara et al. 2003). McNamara et al.'s model investigates the negotiation process between male and female parents, and it assumes that individuals respond repeatedly to the effort of their partner until both parents arrive at a stable negotiated effort. The model predicts that, during biparental care, each parent may not provide the maximum amount of care, to avoid being exploited by the mate. A recent experiment in captive zebra finches, *Taenopygia guttata*, showed that biparental females provide less food per chick and produce lower-quality offspring than uniparental females (Royle et al. 2002). In frigatebirds, the transition from biparental to uniparental care is a natural phenomenon, and the outcome of their sexual conflict over brood care is more evident: once the male has deserted the brood, the sexual conflict is over, and thus, the deserted female can increase her effort.

Female frigatebirds are seemingly in the loser's position as far as sexual conflict is concerned: females always stay with the chick, whereas males are flexible in their brood-rearing strategy. However, a recent model of Barta et al. (2002) showed that females might still be able to manipulate the behaviour of their mates by strategically altering their own body reserves. Barta et al.'s state-dependent dynamic game model describes how male and female parents regulate their body reserves during breeding. This model shows that a parent may keep its own reserves at a low level, so that it can 'force' its mate to provide care. This strategic regulation in a game-theoretic context is a novel and unexpected explanation for changes in body reserves during breeding, because the parent seemingly jeopardizes its own survival to increase the cost of desertion for its mate. In line with the Barta et al. model, a potential explanation for the variable deserting time of male frigatebirds is that male behaviour is manipulated by the female mate. Preliminary data suggest that such strategic body mass regulation may occur in frigatebirds (L. Lee & J. L. Osorno, unpublished data), because biparental females appear to have reduced body mass compared with deserted females (Dearborn 2001; L. Lee & J. L. Osorno, unpublished data). Taken together, these recent theoretical models, and the existing data in frigatebirds (Dearborn 2001; this study) suggest that male and female frigatebirds play a more complex parental care game than previously recognized.

Why might males exploit their females? Exploitation is expected if the benefit of mate retention is low; thus, the male's reproductive success is not tied to the reproductive success of his mate. This is clearly the case in bird species in which one parent frequently abandons the offspring (e.g. Kentish plover, *Charadrius alexandrinus*), because few males keep the same mate between years (Székely & Lessells 1993). Low benefit of mate retention also appears to be the case in magnificent frigatebirds, because adult birds usually mate with a new partner each year (J. L. Osorno, unpublished data).

In conclusion, female frigatebirds contribute more to chick rearing than their mates, although they may still withhold some of their parental effort whilst their mate helps them to feed the chick. We suggest that, by withholding care, the females attempt to force their mates to invest more in brood care. Once the male deserts, the female takes over the full care of the chick, and she fully compensates for the absence of her mate. This contention warrants experimental tests, for instance, by manipulating the food provisioning rates of chicks.

Acknowledgments

We thank A. Lecona, S. Singh, T. Toledo and L. Fernández for their assistance in the field. Fishermen from San Blas and Boca de Camichín and the Mexican Navy kindly provided logistical support and transportation to the island. This project was financially supported by the Consejo Nacional de Ciencia y Tecnología (project number N9208-1614), the Sigma Xi Society and the University of Florida Foundation. The Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) provided the permit to work at the island. J.L.O. visited the University of Bristol through support from the Academia Mexicana de las Ciencias and the Royal Society. T.S. was supported by a travel grant from The Royal Society, and by a grant from the Hungarian Ministry of Higher Education (FKFP-0470/2000). We thank A. Houston, J. McNamara and H. Drummond for their comments on earlier versions of this manuscript.

References

Balshine-Earn, S. & Earn, N. D. J. 1998. On the evolutionary pathway of parental care in cichlid fishes. *Proceedings of the Royal Society of London, Series B*, **265**, 2217–2222.

Bart, J. & Tornes, A. 1989. Importance of monogamous male birds in determining reproductive success: evidence for house wrens and a review of male-removal studies. *Behavioral Ecology and Sociobiology*, **24**, 109–116.

Barta, Z., Houston, A. I., McNamara, J. M. & Székely, T. 2002. Sexual conflict about parental care: the role of reserves. *American Naturalist*, **159**, 687–705.

Bennett, P. M. & Owens, I. P. F. 2002. *Evolutionary Ecology of Birds.* Oxford: Oxford University Press.

Caldow, R. W. G. & Furness, R. W. 2000. The effect of food availability on the foraging behaviour of breeding great skuas *Catharacta skua* and Artic skuas *Stercorarius parasiticus*. *Journal of Avian Biology*, **31**, 367–375.

Calixto, I. & Osorno, J. L. 2000. The diet of the magnificent frigatebird during chick rearing. *Condor*, **102**, 569–576.

Carlisle, T. R. 1982. Brood success in variable environments: implications for parental care allocation. *Animal Behaviour*, **30**, 824–836.

Cezilly, F. 1993. Nest desertion in the greater flamingo, *Phoenicopterus ruber roseus*. *Animal Behaviour*, **45**, 1038–1040.

Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.

Daniel, W. W. 1990. *Applied Nonparametric Statistics*. Boston: PWS-KENT.

Dearborn, D. 2001. Body condition and retaliation in the parental effort decisions of incubating great frigatebirds (*Fregata minor*). *Behavioral Ecology*, **12**, 200–206.

Durand, M. L. 1992. Dimorfismo sexual en la conducta de reproducción y la deserción del macho en Fregata magnificens en la Isla Isabel, Nayarit. B.Sc. thesis, Universidad Nacional Autónoma de México.

Ezaki, Y. 1988. Mate desertion by male great reed warblers *Acrocephalus arundinaceus* at the end of the breeding season. *Ibis*, **130**, 427–437.

Gratto-Trevor, C. L. 1991. Parental care in semipalmated sandpipers *Calidris pusilla*: brood desertion by females. *Ibis*, **133**, 394–399.

Guerra, M. & Drummond, H. 1995. Reversed sexual size dimorphism and parental care: minimal division of labour in the blue-footed booby. *Behaviour*, **132**, 479–496.

Hammerstein, P. & Parker, G. A. 1987. Sexual selection: games between the sexes. In: *Sexual Selection: Testing the Alternatives* (Ed. by W. Bradbury & M. S. Andersson), pp. 119–142. New York: J. Wiley.

Houston, A. I. & McNamara, J. M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.

Kelly, E. J. & Kennedy, P. L. 1993. A dynamic state model of mate desertion in Cooper's hawks. *Ecology*, **74**, 351–366.

McNamara, J. M., Gasson, C. E. & Houston, A. I. 1999. Incorporating rules for responding into evolutionary games. *Nature*, **401**, 368–371.

McNamara, J. M., Houston, A. I., Barta, Z. & Osorno, J. L. 2003. Should young ever be better off with one parent than with two? *Behavioral Ecology*, **14**, 301–310.

Markman, S., Yom-Tov, Y. & Wright, J. 1995. Male parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. *Animal Behaviour*, **50**, 655–669.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Animal Behaviour*, **26**, 1–9.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Nelson, J. B. 1975. The breeding biology of frigatebirds: a comparative review. *Living Bird*, **14**, 113–155.

Osorno, J. L. 1996. Evolution of breeding behavior in the magnificent frigatebird: copulatory pattern and parental investment. Ph.D. thesis, University of Florida.

Osorno, J. L. 1999. Offspring desertion in the magnificent frigatebird: are males facing a trade-off between current and future reproduction? *Journal of Avian Biology*, **30**, 335–341.

Pilastro, A., Bidau, L., Marin, G. & Mingozzi, T. 2001. Female brood desertion increases with number of available mates in rock sparrow. *Journal of Avian Biology*, **32**, 68–72.

Roff, D. A. 1992. *The Evolution of Life Histories*. New York: Chapman & Hall.

Royle, N. C., Hartley, I. R. & Parker, G. A. 2002. Sexual conflict reduces offspring fitness in zebra finches. *Nature*, **416**, 733–736.

Sanz, J. J., Kranenbarg, S. & Tinbergen, J. M. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). *Journal of Animal Ecology*, **69**, 74–84.

Slagsvold, T. & Lifjeld, J. T. 1990. Ultimate adjustment of clutch size to parental feeding capacity in a passerine bird. *Ecology*, **69**, 1918–1922.

Székely, T. & Lessells, C. M. 1993. Mate change by Kentish plovers *Charadrius alexandrinus*. *Ornis Scandinavica*, **24**, 317–322.

Székely, T. & Williams, T. D. 1995. Costs and benefits of brood desertion in female Kentish plovers, *Charadrius alexandrinus*. *Behavioral Ecology and Sociobiology*, **37**, 155–161.

Székely, T., Webb, J. N., Houston, A. I. & McNamara, J. M. 1996. An evolutionary approach to offspring desertion in birds. In: *Current Ornithology*. Vol. 13 (Ed. by V. Nolan, Jr & E. D. Ketterson), pp. 271–330. New York: Plenum.

Székely, T., Webb, J. N. & Cuthill, I. C. 2000. Mating patterns, sexual selection and parental care: an integrative approach. In: *Vertebrate Mating Systems* (Ed. by M. Apollonio, M. Festa-Bianchet & D. Mainardi), pp. 144–223. London: World Science Press.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine-Atherton.

Urano, E. 1992. Early settling the following spring: a long-term benefit of mate desertion by male great reed warblers *Acrocephalus arundinaceus*. *Ibis*, **134**, 83–86.

Webb, J. N., Houston, A. I., McNamara, J. M. & Székely, T. 1999. Multiple patterns of parental care. *Animal Behaviour*, **58**, 983–993.

Weimerskirch, H., Mougey, T. & Hindermeyer, X. 1996. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology*, **6**, 635–643.

Winkler, D. W. & Allen, P. E. 1995. Effects of handicapping on female condition and reproduction in tree swallows (*Tachycineta bicolor*). *Auk*, **112**, 737–747.

Wright, J. & Cuthill, I. 1989. Manipulation of sex differences in parental care. *Behavioral Ecology and Sociobiology*, **25**, 171–181.