Apparent Survival of Adult Magnificent Frigatebirds in the Breeding Colony of Isla Isabel, Mexico

MONICA GONZÁLEZ[1] AND HORACIO DE LA CUEVA[1,2]

[1] Departamento de Biología de la Conservación, Centro de Investigación Científica y Educación Superior
de Ensenada, Km 107, Carretera Tijuana – Ensenada, 22830, México
Mailing address: P.O. Box 434844, San Diego CA, 92143-4844, USA

[2]Corresponding author. Internet: cuevas@cicese.mx

Abstract.—Annual apparent survival rates of the Magnificent Frigatebird (*Fregata magnificens*) were estimated from 1998 to 2003 using a capture-resight model with 870 marked adult birds on Isla Isabel, México (21°51'N, 105°54'W). The most parsimonious model was a time since marking model (or two age class model) with constant resighting rate for males and females (p_m and p_f), constant apparent survival rate for males in both age classes (ϕ^1_m and ϕ^{2+}_m), and time-dependent apparent survival rate for females (ϕ^1_f and ϕ^{2+}_f) in both age classes. We found higher resighting rates in males than in females, a tendency of higher apparent survival in females than in males in 1999, a clear higher apparent survival rates in females than in males in 2000, nearest the same apparent survival rates of the two age classes of males throughout, and differences in apparent survival between age classes of females showing considerable annual variation within age classes. The results suggest permanent emigration of females from the breeding colony, whereas males showed site fidelity. *Received 17 November 2005, accepted 31 October 2006.*

Key words.—Apparent survival rate, emigration, demography, Magnificent Frigatebird, mark-resighting methods, seabirds.

Waterbirds 30(1): 73-79, 2007

Estimates of annual apparent survival rates are fundamental to conservation and management. Apparent (or local) survival rates measure the probability that an individual will survive over a time period, and if alive, return to a sampling site that was previously occupied (Fernandez *et al.* 2003). Mark-resight studies based on live encounter data are a tool for survival estimation (Lebreton *et al.* 1992; Cooke *et al.* 2000; Sandercock 2003), in which individual breeding or displaying birds are captured and marked. Later, marked individuals are sought through intensive recapture or resighting efforts to monitor populations dynamics (Sandercock *et al.* 2000).

The Magnificent Frigatebird, *Fregata magnificens*, is a species listed as high conservation concern by the North American Waterbird Conservation Plan for the Americas (2002), because their populations are considered to be declining and are subjected to known and potential threats (Kushlan *et al.* 2002). Nevertheless, there are no published studies about this species that have quantified the basic population parameters needed for a reliable assessment of population status; these data require long-term studies with several years of marking and resighting.

The Magnificent Frigatebird is a colonial, island-nesting seabird that lays a single egg per breeding season, with a sequentially monogamous mating system. The age of first breeding is unknown, however estimates based on plumage patterns suggest it may take the species from five to seven years to reach maturity (Nelson 1975). The mating process of the Magnificent Frigatebird is based on female choice by visits to, and comparisons between several males (Diamond 1973; Madsen 2005). Nevertheless, the male always chooses and defends his displaying site that invariably becomes the nest site (Osorno 1996). The Magnificent Frigatebird has the longest parental care of all seabirds, and among the Fregatidae family it is the only species where the male always deserts its single offspring (Nelson 1975; Osorno 1996), whereas the female continues feeding the chick after fledging (Osorno and Székely 2004). As a consequence, it has been assumed that males are able to breed every year, whereas successful females may breed in alternate years (Diamond 1972, 1973; Trivelpiece and Ferraris 1987).

On Isla Isabel there is a male-biased operational sex ratio and a male mating success of 57.5% (average over four years; V. Madsen unpubl. data). The breeding season, including displaying, mating, copulation, nesting, and chick rearing, goes from the end of September to April, when males desert the breeding colony. No more than 80% of the breeding-age population attempts to breed each year; unsuccessful adults that either loose their egg or chick rarely attract another mate or construct a new nest on the island during the same breeding season, whereas successful males in the previous breeding season have been seen in reproductive condition close to their previous reproductive site the following breeding season (Osorno 1996). Males and females take part equally in chick rearing up to 49 ± 2.4 days old (Osorno 1996; Lecona 1998). After male desertion the female feeds the chick for another eight months (Osorno 1996, 1999) and when the chick is one year old, the fledging female usually feeds it after sunset likely to avoid kleptoparasitism by co-specifics (M. González, pers. obs.). Thus, only 20% of the Magnificent Frigatebird breeding population is successful in raising a chick in any given year (Osorno 1996) and there are no significant differences in number of fledglings per nest (nesting success) between El Niño and other oceanographic conditions (Solares 2002).

According to Greenwood (1980), in monogamous birds males tend to return to their previous breeding area more than females because, by establishing a territory, males settle in familiar surroundings have breeding advantages. Furthermore, a recurrent finding is that females change sites more often than males after a reproductive failure (Greenwood and Harvey 1982). Since apparent survival rates are comprised of two independent probabilities: true survival (*S*) and site fidelity (*F*), it was expected that (1) higher apparent survival rates would occur among males than females due to the monogamous mating system of frigatebirds and low breeding success of females which may promote permanent emigration of the study area; and (2) higher resighting rates among males than females due to display behavior of males and nocturnal behavior of females.

After six years of mark-resight effort (1998-2003) in the breeding colony of Isla Isabel, Mexico, the main objective in this study was to test predictions about site fidelity and estimate the minimum true survival by quantifying sex-specific annual apparent survival rates as a first step in the knowledge of the species' population dynamics, a basic need for their conservation and management.

METHODS

Study Area

This study was conducted on the largest breeding population of the Magnificent Frigatebird in Mexico (a colony of 35,000-53,400 birds; V. Madsen unpubl. data) at Isla Isabel National Park. Isla Isabel is a 194 ha volcanic island, 28 km off the Central Mexican Pacific Coast (21°51'N, 105°54'W).

During the six-year period between 1998 and 2003, 870 adult frigatebirds (506 males and 364 females) were individually caught by hand at night on their nests and banded in the left ulna with black numbered yellow canvas wing tags covered with nylon, 20.5 × 8 cm and 10.8 g (approximately 1% of the mass of the lightest individuals), and ringed using numbered metal rings. Even though the sample size was 870 frigatebirds, from 1992 to 2003 researchers of the Instituto de Ecología, UNAM marked almost 2,800 Magnificent Frigatebirds at Isla Isabel. It was decided to use only the frigatebirds marked from 1998 to 2003 because the wing tags were new at time of marking, which minimized tag loss during our study. By choosing more recently marked birds, the negative effect in apparent survival rate (ϕ) due to wing tag loss was avoided, and an important mark-resight model assumption was met. To update the encounter histories, since 1998 old wing tags have been replaced and changes in tag number have been registered.

Capture and marking of adult frigatebirds was conducted between 13 February and 23 March 1998 (9 days), 17 October and 13 December 1999 (26 days), 25 September 2000 and 15 May 2001 (54 days), 8 November 2001 and 5 April 2002 (41 days), and 5 October and 12 December 2003 (23 days). Frigatebirds were sexed by feather and body characteristics.

During the breeding season, resighting surveys were conducted by two observers twice a day: between 07.00 and 12.00 h from one high fixed point, and since 15.30 h to sunset from three fixed points over a hill and while walking through the study area. A transect looking for marked frigatebirds through the entire island was made at least once per week. Resighting effort (days spent in field) was uneven among field seasons (Table 1).

Modeling

Adult male and female Magnificent Frigatebirds were coded in capture histories as either not sighted (0) or sighted (1) during all field seasons, and three birds which died immediately after handling and marking were treated as not released on the last handling occasion.

Apparent survival rate (ϕ), the probability that a bird alive at occasion i has survived to occasion i+1 and did

Table 1. Total marked adult Magnificent Frigatebirds, males and females, and capture and resighting effort (days spend in field) by field season at Isla Isabel, México, 1998-2003.

Field Season	Marked adult frigatebirds (*n*)	Males (*n*)	Females (*n*)	Resighting period[1]	Resighting effort (days)
1998	41	13	28		
1999	225	131	94	16 Oct-16 Dec	59
2000	292	162	130	21 Sep-16 Apr[a]	198
2001	168	102	66	23 Sep-7 Mar[b]	93
2002	66	65	1	3 Oct-10 Feb[c]	71
2003	78	33	45	13 Oct-12 Dec	53

[1] In some field seasons, resighting period was extended along the breeding season (from the end of September to April) of the Magnificent Frigatebird: [a]2000-2001; [b]2001-2002; [c]2002-2003.

not permanently emigrate from the study area, as well as resighting rate (*p*), the probability that a bird alive and in the study area in year *i* was detected in year *i* (Fernandez *et al.* 2003), were estimated in two steps. First, a global starting model was selected: a time since marking model ($\phi_{2ac \times t\, x\, sex}$, $p_{t \times sex}$). Apparent survival rates were modeled to account for "two age classes" (2ac) in which apparent survival over the interval immediately following marking (ϕ^1), was estimated separately from apparent survival over all subsequent intervals (ϕ^{2+}), with time dependence (t) for both sexes (sex); whereas resighting rates (*p*) were only modeled with time dependence (t) for both sexes (sex). The MARK 4.1 program was used to perform a parametric Bootstrap goodness of fit (GOF) test of 1,000 simulations to examine the fit of the starting global model to frigatebird data. A variance inflation factor ($\hat{c}$) was calculated as the observed deviance of the global model divided by the mean expected variance from the results of bootstrap simulations to quantify the amount of overdispersion, the sampling variance exceeding the theoretical model-based variance (Burnham and Anderson 1998). If $\hat{c} = 1$ the model fits the data, if $\hat{c} > 1$, then there is a lack of fit (Lebreton *et al.* 1992; Burnham and Anderson 1998). Moderate amounts of overdispersion are common in analyses of mark-recapture/resight data and values of $\hat{c}$ between 1 and 3 indicate that the global model is acceptable (Sandercock *et al.* 2005).

Second, a hierarchical procedure similar to that of Sandercock *et al.* (2005) was followed to guide the nested models construction. Because the primary interest was apparent survival, resighting rate was modeled first as a nuisance parameter; thus, resighting rates were modeled to find the best fit for *p* before modeling apparent survival rates. Starting with the global model, constraints to the probabilities were applied as follows: resighting rates (*p*), apparent survival of two age classes of both sexes (2ac), apparent survival of two age classes of males (ϕ^1_m, ϕ^{2+}_m), and apparent survival of two age classes of females (ϕ^1_f, ϕ^{2+}_f). Overdispersion was corrected by using the $\hat{c}$-value to improve parameter estimations (Burnham and Anderson 1998). The quasi-Akaike Information Criterion ($QAICc = -(Dev/\hat{c}) + 2K + 2K(K+1)/(n-K-1)$, where Dev is the model deviance, K is the number of parameters and n is sample size was used to select models based on the difference in QAICc values between models (ΔQAICc) and Akaike weights (w*i*) (Burnham and Anderson 1998):

$$wi = \exp(-0.5\Delta_i) / \sum_{Ri=1}^{R} \exp(-0.5\Delta_r)$$

Finally, the principle of parsimony, bias versus variance trade off (Lebreton *et al.* 1992, Burnham and Anderson 1998), was used to select the most parsimonious model by minimum ΔQAICc value. Annual parameters for males and females were estimated using the model averaging procedure of MARK 4.1, where parameter estimates were weighted by the Akaike weight of the model for which they were derived. Estimates of variance include the conditional sampling variance and the variation associated with the uncertainty of the model. A logit-link function was used to construct all models. Parameter estimates are presented as mean ± SE.

RESULTS

The bootstrap goodness-of-fit test ($P < 0.01$), gave a variance inflation factor $\hat{c} = 1.70$; thus, the global model was acceptable. Differences in resighting effort among field seasons did not affect the resighting rate. The model considering resighting effort (Model 2; Table 2) was better supported by the data than the underlying model (Model 1; Table 2). The apparent survival of males and females was different in the interval followed marking ($\hat{\phi}^1$) from the all subsequent intervals ($\hat{\phi}^{2+}$), mainly in females, since all models considering time since marking were more parsimonious than the model without this effect (Model 7; Table 2). A model in which resighting rate was considered constant through time for both sexes and apparent survival rate was considered affected by time since marking (Model 12; Table 2) was the best supported model. In this model, apparent survival of the two "age classes" of males was constant throughout time, while apparent survival of the two "age classes" of females varied over time.

The arithmetic mean of the weighted averaging across all candidate models (Table

Table 2. Fit of the global and reduced models for estimating apparent survival (ϕ) and resighting rates (p) of adult male and female Magnificent Frigatebirds breeding at Isla Isabel, México (1998-2003).

	Model Statistics[b]					
Models[a]	QAICc	ΔQAICc	W_i	K	QDev	Model Description[a]
Modeling p						
1. $\phi_{2ac \times t \times sex}$, $p_{t \times sex}$	1708.50	20.2	0.00002	25	79.0	Time-dependent by sex.
2. $\phi_{2ac \times t \times sex}$, $p_{e \times sex}$	4824.20	3136.0	0.00000	16	3213.2	Resighting effort (e) effect by sex
3. $\phi_{2ac \times t \times sex}$, $p_{t + sex}$	1703.20	15.0	0.00033	22	80.0	Time-dependent without time × sex interaction.
4. $\phi_{2ac \times t \times sex}$, p_{t}	1702.20	14.0	0.00056	21	81.0	Time-dependent without sex structure.
5. $\phi_{2ac \times t \times sex}$, p_{sex}	1698.10	9.9	0.00426	18	83.0	Time constant in both sexes
Modeling ϕ						
6. $\phi_{2ac + t \times sex}$, p_{sex}	1701.30	13.0	0.00089	14	94.4	2ac with out time × age interaction within sex.
7. $\phi_{t \times sex}$, p_{sex}	1701.84	14.6	0.00066	12	99.0	Without two age class effect
8. $\phi_{2ac(t/c) \times sex}$, p_{sex}	1699.10	10.8	0.00263	13	94.2	ϕ^1 time-dependent, ϕ^{2+} constant through time (t/c) in both sexes.
9. $\phi_{2ac(c/t) \times sex}$, P_{sex}	1694.40	6.2	0.02690	12	91.6	ϕ^1 constant through time, ϕ^{2+} time-dependent (c/t) in both sexes.
10. $\phi_{m(c/t), f(t)}$, p_{sex}	1693.00	4.7	0.05570	14	86.1	Male ϕ^1 constant through time, male ϕ^{2+} time-dependent (c/t). Female 2ac time-dependent (t).
11. $\phi_{m(t/c), f(t)}$, p_{sex}	1693.80	5.5	0.03745	15	84.8	Male ϕ^1 time-dependent, male ϕ^{2+} constant through time (t/c). Female 2ac time-dependent (t).
12. $\phi_{m(c), f(t)}$, p_{sex}	1688.30	0.0	0.58856	11	87.5	Male 2ac constant through time (c). Female 2ac time-dependent (t).
13. $\phi_{m(c), f(c/t)}$, p_{sex}	1689.70	1.5	0.28203	9	93.0	Male 2ac constant through time (c). Female ϕ^1 constant trough time, ϕ^{2+} time-dependent (c/t).

[a] Model Notation and Model description: ϕ_{2ac}: survival estimated over the interval immediately following marking (ϕ^1), and survival estimated over all subsequent occasions (ϕ^{2+}). ϕ_m, apparent survival rate of males; ϕ_f, apparent survival rate of females.

[b] Model Statistics included: quasi-Akaike's Information Criterion (QAICc), QAICc differences (ΔQAICc), QAICc Weight (w_i), number of parameters (k), and deviance (QDEV).

3) showed higher resighting rate for males than for females in all intervals ($\hat{p}_m = 0.75 \pm 0.07$ *vs.* $\hat{p}_f = 0.70 \pm 0.04$) and nearly the same apparent survival rates of the "two age classes" of males ($\hat{\phi}^1_m = 0.86 \pm 0.04$, $\hat{\phi}^{2+}_m = 0.84 \pm 0.04$). There was considerable annual variation of apparent survival rates of females between and within age classes ($\hat{\phi}^1_f = 0.21 \pm 0.31\text{-}0.75 \pm 0.10$; $\hat{\phi}^{2+}_f = 0.71 \pm 0.22 - 1.00 \pm 0.04$) and whereas the results suggest an effect of greater apparent survival rates of females than males in 1999, this difference was clear in 2000 (Table 3).

DISCUSSION

This is the first quantification of the apparent survival in the Magnificent Frigatebird. The major results show: (1) constant apparent survival rate within the two age classes of males likely because of the site fidelity behavior showed by them; (2) a tendency for apparent survival rate of females to exceed that of males in the intervals after marking ($\hat{\phi}^{2+}$) in 1999, which becomes clear in 2000, and due either to emigration of females being low due to a successful previous

Table 3. Model averaged annual apparent survival rate for the interval after first capture (ϕ^1) and later occasions (ϕ^{2+}), and resighting rate (*p*), both mean ± SE, of adult male and female Magnificent Frigatebirds. Breeding seasons 1998-2003, Isla Isabel, México.

	ϕ^1		ϕ^{2+}		(*p*)	
Season[a]	Males	Females	Males	Females	Males	Females
1998	0.86 ± 0.05	0.60 ± 0.12			0.75 ± 0.03	0.70 ± 0.04
1999	0.86 ± 0.06	0.61 ± 0.07	0.85 ± 0.06	0.93 ± 0.12	0.75 ± 0.02	0.70 ± 0.04
2000	0.86 ± 0.03	0.72 ± 0.06	0.85 ± 0.03	1.00 ± 0.04	0.75 ± 0.02	0.70 ± 0.04
2001	0.87 ± 0.03	0.75 ± 0.10	0.84 ± 0.03	0.75 ± 0.06	0.75 ± 0.02	0.70 ± 0.04
2002	0.86 ± 0.28	0.21 ± 0.31	0.84 ± 0.03	0.71 ± 0.22	0.75 ± 0.26	0.70 ± 0.26
$\bar{x}$	0.86 ± 0.04	0.58 ± 0.13	0.84 ± 0.04	0.85 ± 0.11	0.75 ± 0.07	0.70 ± 0.08

[a] Season: starting year of interval (e.g., 1998 = 1998-1999).

breeding year or because there was a high true survival of females; (3) apparent survival rate $\hat{\phi}^{2+} > \hat{\phi}^1$ and highly time-dependent apparent survival rate within intervals of females that suggests permanent emigration of females likely due to unsuccessful breeding (either due to handling effect, intra-specific competition or other factors); and, (4) a higher resighting rate for males than for females likely due to male displaying behavior and female nocturnal behavior as was hypothesized.

A time since marking model fits the data of Magnificent Frigatebirds because it allowed control for birds that were never detected after the year of marking, which can be evidence of: (1) handling effect on survival or site fidelity, whereas some frigatebirds ($\hat{\phi}^1$) were affected by handling, other frigatebirds ($\hat{\phi}^{2+}$) may not suffer this effect. (2) Age. Even though males and females were marked as adult birds, their age at time of capture was unknown, so it was possible that we marked adults in their first breeding attempt and adults with several breeding years of experience. Adults are much more faithful to a breeding territory or colony than young birds seeking their first breeding opportunity, and in many cases the majority of adults will re-occupy or retain their site of previous years (Greenwood 1987). (3) Presence of transients. Since transients are very common in natural populations (Pradel *et al.* 1997), a sample of newly marked frigatebirds could include resident and transient individuals, whereas subsequent resights involved residents only.

Apparent Survival Rates

After their mate deserts, females nearly double their feeding rates to compensate for the loss (Osorno and Szekély 2004). This may have energetic costs that could result in a lower survival for females than for males. Since apparent survival is a composite probability when it is used to make comparisons among sexes, apparent survival may reflect variation in true survival (S) or site fidelity (F). Thus, the tendency of higher apparent survival rates ($\hat{\phi}^{2+}$) of females than those of males suggested by our results in 1999 and the clear difference found in 2000, may be due to (1) the previous intervals (1998 and especially 1999) were breeding successful years for females leading them to stay on the island until the next breeding season without the need to emigrate or (2) because indeed, males had a lower true survival than females in those years.

The opposite phenomenon could have occurred in 2001 and 2002 when the apparent survival of males exceeded that of females. Possibly, the previous intervals were unsuccessful breeding years for females leading them to emigrate permanently, or there was a lower true survival of females than males.

The constant apparent survival rate within and among the two age classes of males, were likely because males showed a high site fidelity to the study area. In six years of daily resighting we did not locate any marked males nesting on other sites on the island, only in the study area. Since in monogamous systems males are usually philopatric, resourcedefense needs can include nesting sites and roosting areas (Greenwood 1983).

Because Magnificent Frigatebirds are highly aerial, males and females were caught for marking when they were on the nest (incubating or with a chick). A handling effect on breeding success of females leading them to emigrate, could explain the lower apparent survival rates of females in the interval immediately following marking ($\hat{\phi}^1$) than in the over all subsequent intervals ($\hat{\phi}^{2+}$). A frequent finding from a wide range of birds species is that individuals move to a new breeding locality following a poor or unsuccessful breeding attempt in the previous year (e.g. *Acrocephalus scirpaceus, A. shoenobaenus, Parus major*, and *Rissa tridactyla*; Greenwood and Harvey 1982). In some species of penguins and warblers, females change sites more often than males after reproductive failure (Greenwood and Harvey 1982). Furthermore, because 80% of frigatebird females fail in rearing their chick any given year mainly due to intraspecific competition over already constructed nests (Osorno 1996), differences in annual apparent survival rates within the "age classes" of females could be a result of permanent emigration to new breeding localities after breeding failure. We have been informed of the presence of some marked females breeding on Camichin, Nayarit (28 km from Isla Isabel), in the Central Mexican Pacific Coast. Also two marked frigatebirds have been observed breeding in Bahía Santa María, Sinaloa (González-Bernal, pers. comm.) in Central Mexican Pacific Coast (25°00'N, 108°10'W).

Even though there is neither evidence for sex-biased mortality or estimates of adult mortality on Magnificent Frigatebirds, this study provides minimum estimates of true survival through annual apparent survival calculations (ϕ), mainly for males due to their site-faithfulness. Until now the most important known causes of mortality for adults nesting in Isla Isabel are (1) shooting by shrimp fisherman, (2) on Isla Isabel, birds get stuck between tree branches, falling to the ground without chance of taking off, and some collide in flight breaking a wing (M. González, pers. obs.). Because the most important foraging strategies on the colony are opportunistic feeding on prawn-fishing boats (Calixto-Albarrán and Osorno 2000), followed by direct surface fishing, kleptoparasitism on blue footed boobies, *Sula nebouxii* (Osorno *et al.* 1992), and predation on chicks of blue footed and brown boobies, *S. leucogaster* (M. González, pers. obs.), breeding adult Magnificent Frigatebirds on Isla Isabel rarely die of starvation. In six years of study we have only found starving juveniles.

Resighting Rates

Resighting effort was constrained mostly to the courtship season between October and December, when male courtship behavior makes wing marks of males more visible than those of females (females have no ritualized wing actions). Even though there was a daily intensive resighting effort of overflying, roosted, nesting, and breeding frigatebirds on the main study area and the entire island throughout the length of the study, and we registered daily overflying frigatebirds not only during the scheduled resighting effort but also in our spare time, there is a chance that some marked females were not detected. This way, the higher resighting rate in males than in females likely was due to greater conspicuousness of male markings and nocturnal behavior of females as was predicted.

There was not an effect of differences in resighting effort among years on the resighting rate, as it is supported by model comparisons (Model 1 vs. Model 2; Table 2), which in turn suggest that detection probability was high enough for frigatebirds present on the study area. Since the probability of temporarily moving out of the study site results in a lower detection probability (Pradel *et al.* 1997), the lack of relationship between resighting effort and resighting rate may suggest temporary emigration among residents. Nevertheless, we have not strong evidence to support this assumption.

ACKNOWLEDGMENTS

We thank Vinni Madsen for her help, advice, and data; Brett Sandercock, Guillermo Fernández, and an anonymous reviewer for their advice on modeling and valuable comments on our manuscript. José Luis Osorno provided financial support and dedicated assistance in research design; L. Lee, A. J. Nieto, N. Palomo, M. Serrano, E. Tobón, and C. Woolf from the Laboratorio de Conducta Animal, Instituto de Ecología, UNAM provided us with data of marked frigatebirds. The administrators of Isla Contoy and Isla Isabel National Parks gave us all the facilities to visit and work at the islands; PRONATURA, Sinaloa provided logistic support and staff to visit Isla Tunitas; the Mexican Navy and the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) provided logistic support to work at Isla Isabel. Fishermen of San Blas and Boca de Camichin helped us in unaccountable ways. We thank to all volunteers in this project.

LITERATURE CITED

Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference, A Practical Information-Theoretic Approach. Springer Verlag, New York.

Calixto-Albarran, I. and J. L. Osorno. 2000. The diet of the Magnificent Frigatebird during chick rearing. Condor 102: 569-676.

Cooke, F., G. J. Robertson, C. M. Smith, R. I. Goudie and W. W. Boyd. 2000. Survival, emigration, and winter population structure of harlequin ducks. Condor 102: 137-144.

Diamond, A. W. 1972. Sexual dimorphism in breeding cycles and unequal sex ratio in magnificent frigatebirds. Ibis 114: 395-398.

Diamond, A. W. 1973. Notes on the breeding biology and behavior of the Magnificent Frigatebird. Condor 75: 200-209.

Fernández, G., H. de la Cueva, N. Warnock and D. B. Lank. 2003. Apparent survival rates of Western Sandpiper (*Calidris mauri*) wintering in northwest Baja California, México. Auk 120: 55-61.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 1140-1162.

Greenwood, P. J. 1983. Mating systems and the evolutionary consequences of dispersal. Pages 132-159 *in* The Ecology of Animal Movement (I. R. Swingland and P. J. Greenwood, Eds.). Claredon Press, Oxford.

Greenwood, P. J. 1987. Inbreeding, philopatry and optimal outbreeding in birds. Pages 207-222 *in* Avian Genetics (Cooke F. and P. A. Bucley, Eds.). Academic Press, London.

Greenwood, P. J. and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13: 1-21.

Kushlan, J. A., M. J. Steinkamp, K. C. Parsons, J. Capp, M. Acosta-Cruz, M. Coulter, I. Davidson, L. Dickson, N. Edelson, R. Elliot, R. M. Erwin, S. Hatch, S. Kress, R. Milko, S. Miller, K. Mills, R. Paul, R. Phillips, J. E. Saliva, B. Sydeman, J. Trapp, J. Wheeler and K. Wohl. 2002. Waterbird Conservation for the Americas: The North American Waterbird Conservation Plan, Version 1. Waterbird Conservation for the Americas, U.S. Fish and Wildlife Service National Publications Clearinghouse. Washington, D.C.

Lebreton, J. D., K. P. Burnham, J. Clobert and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67-118.

Lecona, A. A. 1998. Discriminación parental en *Fregata magnificens* de Isla Isabel, Nayarit. Unpublished B.Sc. Thesis. Universidad Nacional Autónoma de México.

Madsen, V. 2005. Female mate choice in the Magnificent Frigatebird (*Fregata magnificens*). Unpublished Ph.D. Thesis. Universidad Nacional Autónoma de México. México D.F.

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. Unpublished 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.

Osorno, J. L. and T. Székely. 2004. Sexual conflict and parental care in Magnificent Frigatebirds: full compensation by deserted females. Animal Behaviour 68: 337-342.

Osorno, J. L., R. Torres and C. Macias-García. 1992. Kleptoparasitic behavior of the Magnificent Frigatebird: sex bias and success. Condor 94: 692-698.

Pradel, R., J. E. Hines, J. D. Lebreton and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. Biometrics 53: 60-72.

Sandercock, B. K. 2003. Estimation of survival rates for wader populations: a review of mark-recapture methods. Wader Study Group Bulletin 100: 163-174.

Sandercock, B. K., T. Székely and A. Kosztolányi. 2005. The effects of age and sex on the apparent survival of Kentish Plovers breeding in southern Turkey. Condor 107: 583-596.

Sandercock, B. K., S. R. Beissinger, S. H. Stoleson, R. R. Melland and C. R Hughes. 2000. Survival rates of a neotropical parrot: implications for latitudinal comparisons of avian demography. Ecology 81: 1351-1370.

Solares, V. E. 2002. Variación geográfica en los patrones de cuidado parental en *Fregata magnificens.* Unpublished B.Sc. Thesis. Universidad Nacional Autónoma de México, México D.F.

Trivelpiece, W. Z. and J. D. Ferraris. 1987. Notes on the behavioural ecology of the Magnificent Frigatebird *Fregata magnificens.* Ibis 129: 168-174.