



*Male Magnificent Frigatebird landing near the nest on Ilhéu de Curral Velho Bij het nest landende man Amerikaanse Fregatvogel op Ilhéu de Curral Velho (P. López Suárez)*

# RESTRICTED NESTING HABITAT AND REPRODUCTIVE FAILURE OF MAGNIFICENT FRIGATEBIRDS *FREGATA MAGNIFICENS* IN THE CAPE VERDE ISLANDS

PEDRO LÓPEZ SUÁREZ<sup>1,2,4</sup>, NURIA VARO CRUZ<sup>1,2</sup>, CORNELIS J.  
HAZEVOET<sup>3</sup> & LUIS FELIPE LÓPEZ JURADO<sup>1,2</sup>

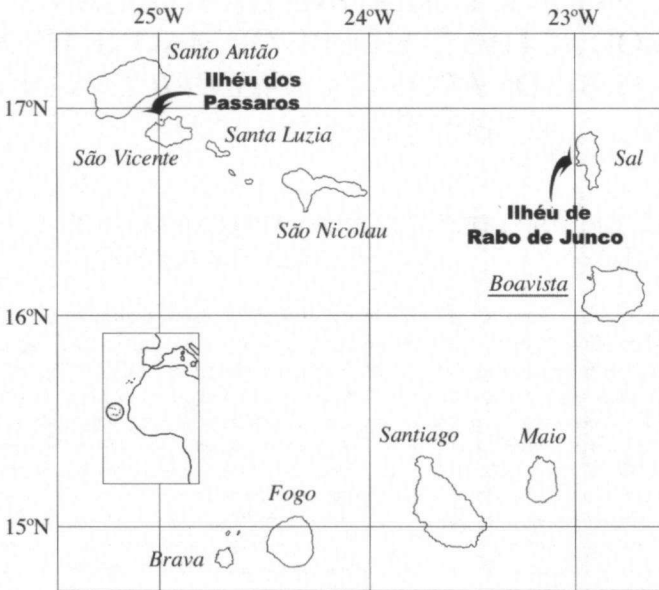
López Suárez P., Varo Cruz N., Hazevoet C.J. & López Jurado L.F. 2005. Restricted nesting habitat and reproductive failure of Magnificent Frigatebirds *Fregata magnificens* in the Cape Verde Islands. *Atlantic Seabirds* 7(3): 107-120. *The islets of Baluarte and Curral Velho, off the island of Boavista, Cape Verde Islands, are the only two breeding sites of the Magnificent Frigatebird Fregata magnificens in the Western Palearctic. This East Atlantic relict population was monitored from the summer of 1999 up to May 2006. Most surveys were conducted during the breeding season, i.e. from November to June. Total reproductive failure has been the rule over the last seven consecutive breeding seasons. Possible causes of nest failure are attributed to: 1) accidental egg loss during the incubation period; 2) hatching failure. The most plausible reasons explaining both causes are discussed. Human persecution and disturbance, restricted nesting habitat and isolation, and unsuccessful breeding has brought the population on the verge of extinction. The remaining population, thought to consist of 4-5 adult individuals (2 females and 2-3 males), is unlikely to survive on its own.*

<sup>1</sup>Cabo Verde Natura 2000, P.O. Box 100, Boavista, Republic of Cape Verde;

<sup>2</sup>Departamento de Biología, Universidad de Las Palmas de Gran Canaria, Apdo. 550, 35080 Las Palmas de Gran Canaria, Spain; <sup>3</sup>Museu Nacional de História Natural, Rua da Escola Politécnica 58, 1250 Lisboa, Portugal; <sup>4</sup>Corresponding author, e-mail: curral\_velho@hotmail.com

## INTRODUCTION

Frigatebirds *Fregata* form a group of five closely related species (Nelson 1975; Harrison 1983; Sibley and Monroe 1990). The Magnificent Frigatebird *Fregata magnificens* is distributed along eastern Pacific and western Atlantic coasts from Baja California to Ecuador, including the Galapagos Islands, and from Florida to southern Brazil. A small relict population survives in the Cape Verde Islands (del Hoyo *et al.* 1992), the only breeding locality in the Western Palearctic (Fig. 1). The fact that frigatebirds rely on thermals for flight may explain why these birds are restricted to trade-wind zones, where soaring conditions are optimal throughout the year. Morphology and flight proficiency of these birds, together



*Figure 1. Map of the Cape Verde Islands.*

*Figuur 1. Plattegrond van de Kaap Verdische Eilanden.*

with other traits such as foraging strategy, breeding biology and life expectancy (more than 30 years) also appear to be adaptations to tropical waters of limited productivity (Weimerskirch *et al.* 2003).

Frigatebirds are monogamous and rear a single highly altricial chick (Diamond 1972, 1973; Nelson 1975). In general, they do not stay with the same mate or at the same nesting site from year to year. Each new breeding effort involves establishing a new territory and nesting site as well as finding a new mate. The breeding cycle (12-18 months) is amongst the longest in seabirds (Nelson 1975; Osorno 1996) and is characterized by a long egg-laying period, slow growth and development of the single chick, the extraordinary length of post-fledging care (Stonehouse & Stonehouse 1963; Nelson 1967; Schreiber & Ashmole 1970; Diamond 1972, 1973, 1975), and the difficulty adults have in obtaining sufficient food for their young over such a long period (Nelson 1975). Both members of a pair take their turn in incubating and foraging. Incubating birds fast while on the nest and cannot leave until their mate returns. A

successful breeding attempt thus requires coordination of incubating shifts (Dearborn 2001).

In the Magnificent Frigatebird, both parents equally share incubation and the first three weeks of brooding (Nelson 1975; Durand 1992; Osorno 1996). However, while the chick is still young (20-110 days), the male departs and leaves the female to feed the chick for the remaining 9-12 months (Diamond 1972, 1973; Osorno 1996). The timing of desertion may be a trade-off between current and future reproduction, constrained by settling date and a presumed long-lasting moult or recovery period (Osorno 1999). Fledging takes from 4.5-7 months, while post-fledging care probably lasts 9-12 months (Nelson 1975). When successful, females breed bi-annually, while males may breed annually (Diamond 1972, 1973; Nelson 1975; Trivelpiece & Ferraris 1987; Osorno 1999). Most breeding occurs on small, remote islands, free from human disturbance and terrestrial predators. Mangroves and other trees and bushes are the favourite sites, both for nesting and roosting. All over the species' range, laying has been recorded all year round, with a preference for the local dry season, which often coincides with the onset of trade winds. The species is highly gregarious at breeding and roosting sites and often appears in mixed colonies alongside other species of Pelecaniformes (del Hoyo *et al.* 1992). Available data indicate that the breeding season in the Cape Verde Islands is prolonged (Cramp & Simmons 1977, Hazevoet 1995).

Although the species may have bred on islets off São Vicente (Ilhéu dos Pássaros) and Sal (Ilhéu de Rabo de Junco) (Fig. 1) in the past (Hazevoet 1995), nesting is now confined to two islets off Boavista, i.e. Ilhéu de Baluarte, off the eastern coast, and Ilhéu de Cural Velho, off the southern coast (Fig. 2), with wanderers occasionally occurring throughout the archipelago, as well as off western Africa (Bannerman & Bannerman 1968, de Naurois 1969, Cramp & Simmons 1977, Hazevoet 1995).

The total world population is probably several 100,000 birds (Nelson 1975). Although probably never particularly numerous, the Cape Verde population has severely declined over the last decades. Direct persecution, particularly by fishermen, along with habitat destruction and human disturbance have been identified as the main causes of this decline, not only of the Cape Verde frigatebirds, but also of other seabird populations in the archipelago (Bannerman & Bannerman 1968, del Hoyo *et al.* 1992, Hazevoet 1994, 1995).

The aim of the present study was to establish the precise size of the population of Magnificent Frigatebirds in Cape Verde, define the breeding period, assess the reproductive success, collect other data on the biology of the species and identify conservation problems.

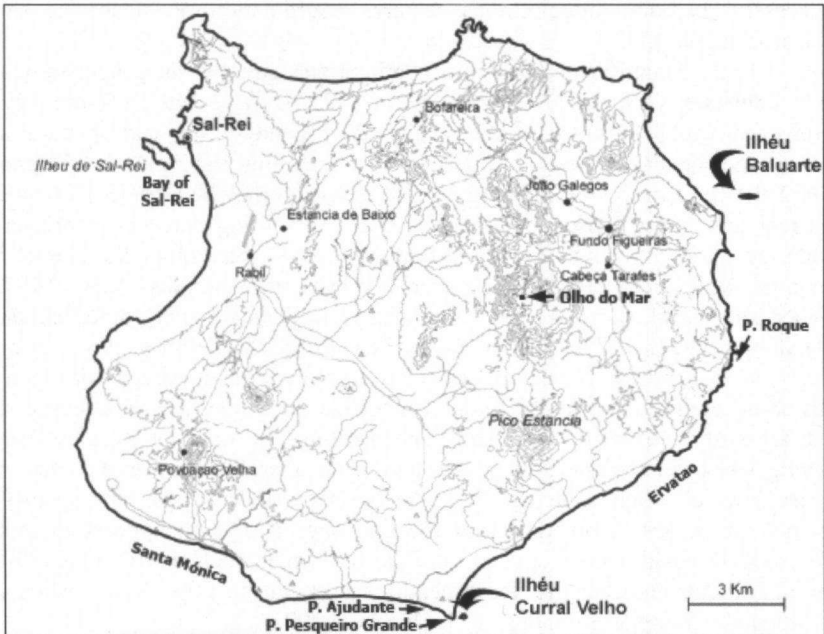


Figure 2. Map of Boavista, showing localities mentioned in the text.

Figuur 2. Kaart van Boavista, inclusief de plaatsen die in de tekst genoemd worden.

## METHODS

**Study Area** Located one mile off the eastern coast of Boavista, Ilhéu de Baluarte (16°09'N, 22°39'W) is a nesting site for Brown Booby *Sula leucogaster* and Magnificent Frigatebird. The flat and low-lying islet (0.07 km<sup>2</sup>) consists of two differentiated areas: a central stony plateau with sparse creeping vegetation and a peripheral zone constituted of rocks and boulders. The latter area is subject to floods during spring-tide and storms. Because of its easy accessibility, the islet is frequently raided by fishermen who take booby eggs and chicks. At present, the booby colony does not hold more than 20-30 pairs.

The whitish, calcareous and eroded islet of Curral Velho (15°58'N, 22°47'W) emerges abruptly c. 500 m off the southern coast of Boavista. The surface area of the islet is c. 0.006 km<sup>2</sup>. Most of its shoreline is a low cliff, less than 10 m high, and the islet is devoid of vegetation. Apart from Brown Boobies and Magnificent Frigatebirds, the endemic Cape Verde Shearwater *Calonectris*

*edwardsii* also nests on the islet. The booby colony has 100-120 breeding pairs, whereas de Cape Verde Shearwater population consists of 60-70 pairs. Other seabirds have also been reported from the islet, i.e. Cape Verde Little Shearwater *Puffinus boydi* and Madeiran Storm-Petrel *Oceanodroma castro* (de Naurois 1969, Hazevoet 1995), while a few pairs of Red-billed Tropicbirds *Phaethon aethereus* are known to nest at Ponta Pesqueiro Grande and Ponta de Ajudante, on the adjacent coast of Boa Vista (Fig. 2), and may occasionally also use the walls of the islet for nesting. Access is difficult, preventing Ilhéu de Curral Velho from being raided frequently, although seabird eggs and chicks are known to be taken occasionally.

**Surveys** Available data indicated that breeding activity of frigatebirds in Cape Verde starts with the onset of the dry season, i.e. November. The population was monitored during seven consecutive breeding seasons: 1999-2000, 2000-2001, 2001-2002, 2002-2003, 2003-2004, 2004-2005 and 2005-2006. Ilhéu de Curral Velho was surveyed on 43 occasions, whereas Ilhéu de Baluarte was visited 28 times. Differences in survey effort between the two islets are mainly due to the fact that frigatebirds nested more often on Curral Velho than on Baluarte. The islets were chiefly visited during the breeding season, provided that this was logistically feasible. Access to Baluarte is only possible by boat. When no boat was available and sea conditions were sufficiently safe, Curral Velho was reached by swimming from the adjacent coast of Boavista.

## RESULTS

The lack of suitable vegetation on Baluarte and Curral Velho force frigatebirds to nest on the ground, with nesting material (small sticks) brought to the islets from the main island of Boavista (Bannerman & Bannerman 1968; del Hoyo *et al.* 1992; Hazevoet 1995). Ascension Frigatebird *F. aquila* also nests on bare ground (Stonehouse & Stonehouse 1963), as does Lesser Frigatebird *F. ariel* (Reville 1991). Nesting has never been reported on Baluarte and Curral Velho simultaneously and only in the 2002-2003 season did frigatebirds nest on Baluarte. In the remaining six seasons, nesting was restricted to Curral Velho.

During every single season, two nests were found, always less than 2 m apart from each other. As indicated by the presence of eggs, egg-laying may extend from November to May. To minimize disturbance, birds were never intentionally displaced from their nests to verify the presence of eggs or nestlings, making it difficult to accurately define the egg-laying period. Nonetheless, it is likely that laying mostly occurs from November to March. The irregular survey effort made it impossible to establish the possible

replacement of lost eggs. Nonetheless, we do not think that such replacement occurred, since egg loss was usually followed by desertion of the nest-sites.

Elsewhere on Boavista, frigatebirds frequently visit the bay of Sal Rei and are often sighted off Santa Mónica, Ervatão and Ponta de Roque (Fig. 2). In contrast, sightings along the northern coast of Boavista are rare. Frigatebirds were also observed drinking fresh water from a pool at Olho do Mar (Fig. 2), in a mountainous area c. 8 km from the nearest shore. The habit of drinking fresh water, when available, distinguishes frigatebirds from most other seabirds (del Hoyo *et al.* 1992). Apart from the islets of Baluarte and Curral Velho, Ponta de Roque is the only known roosting site.

A summary of the main events observed during every single season is given in the Appendix.

## DISCUSSION

**Population size** The Cape Verde frigatebird population has declined rapidly during the last decades. In 1965, de Naurois (1969) estimated the total breeding population on Ilhéu de Curral Velho to be 10-12 pairs. During the years 1988-1992, no more than five pairs were present on Baluarte and Curral Velho together (Hazevoet 1995), while Noeske *et al.* (1994) reported two breeding pairs on Curral Velho in 1993. All of these figures were based on opportunistic observations rather than systematic surveys.

Based on sightings on Baluarte, 30 June 1999, and Curral Velho, 12 April 2000, the frigatebird population of Cape Verde was judged to consist of five adult birds, i.e. three males and two females. Six birds (four males – two of which in breeding condition – and two females), perching on two nests, were seen on Baluarte, 6 April 2003 (Colin & Geiregat 2003). The find of a dead male on 25 January 2005 on the same islet reduced the population again to five birds. As of May 2006, the population is reckoned to comprise just four birds. In April 2004, three males were seen for the last time during a single survey. During the last two breeding seasons (2005-2006), a maximum of two females and two males was counted, all on Curral Velho.

Of particular significance was the sighting of an immature bird flying over Curral Velho in April 2006. No young birds were observed in the late 1980's and early 1990's (Hazevoet 1994, 1995), although Noeske *et al.* (1994) stated that a small number of immatures remained around the archipelago, without, however, providing further details to support their assertion. Young frigatebirds attain adult plumage in their fourth year (Gibson-Hill 1947) and first breeding occurs when they are at least 5-7 years, possibly older (Nelson 1975). In view of these observations and the reproductive failure since the 1999-2000

season, it does not seem likely that this immature fledged in Cape Verde. Immature frigatebirds may disperse several thousands of kilometres from the nesting area (Nelson 1975), wandering widely until reaching breeding age (Hill & Dunn 2004). It seems reasonable to presume that immature specimens sighted in Cape Verde are transatlantic vagrants from the western Atlantic. Seabirds, although capable of travelling enormous distances, often exhibit great natal site fidelity (Fisher 1976; Schreiber & Schreiber 1993; Austin *et al.* 1994; Schørring 2001; Bried & Jouventin 2002; Weimerskirch *et al.* 2006). Thus, it seems likely that movements of individuals from the western to the eastern Atlantic are due to juvenile dispersion, with a negligible effect on Cape Verde population size (through recruitment) and genetic structure (through effective gene flow).

**Breeding success** In frigatebirds, breeding failure may amount to 80-85% (Nelson 1975). In southern Baja California, 46% of eggs and chicks of Magnificent Frigatebird were lost (Carmona *et al.* 1995), while in Great Frigatebird *F. minor*, Dearborn (2001) found a rate of nest failure during incubation of over 50%. In Christmas Island Frigatebird *F. andrewsi* probably only 15-20% of eggs yield fledged young (Hill & Dunn 2004).

In Cape Verde, no offspring was reported during the last seven years – the 11 confirmed eggs all failed to hatch. Reproductive failure causes females to begin a breeding cycle each year. The presence of two eggs was confirmed in four out of the seven nesting seasons (see Appendix), but we cannot rule out that two eggs were also laid in 2002-2003 and 2004-2005. In 2002-2003, Baluarte was only visited late in the nesting season. During the 2004-2005 season, nest 1 was occupied during three consecutive monthly surveys, which may indicate that an egg was being incubated. However, despite intensive monitoring of Curral Velho in November–July, we do not have clear evidence that two eggs were laid in the 2003-2004 season.

Direct causes of nest failure in frigatebirds include egg loss and mortality of small young which may result from conspecific interference (Nelson 1975), such as competition for perching sites (Trivelpiece & Ferraris 1987), usurpation of nests by unpaired males (Reville 1988; Dearborn 2001), and males competing for or stealing nesting material (Dearborn 2001). Often, these interactions appear to be triggered by human disturbance. Landing of people on the islets disturbs the boobies, whose flight behaviour alerts the frigatebirds. As a result, frigatebirds on the nest or incubating an egg may take flight as well and engage in inter- (with boobies) and intraspecific aggressive interactions. Unbalanced sex ratio in the Cape Verde frigatebird population could cause usurpation of nests and competition for nesting material and intruding males may dislodge eggs, as observed on Curral Velho on 11 April 2001 (See Appendix).



Dearborn (2001) pointed out that the main causes of nest failure in frigatebirds during incubation likely increase because of the prolonged absence of the foraging member of the pair. In such circumstances, the incubating bird may weaken, being less able to fend off aggressors. Long incubation shifts may lead to depletion of the incubator's body reserves and force desertion of the egg or chick (Davis 1982; Erickstad *et al.* 1997; Monaghan *et al.* 1992; Weimerskirch 1995). Nonetheless, in view of the small population size in relation to the feeding area, Cape Verde frigatebirds are unlikely to be subject to such feeding vicissitudes (Diamond 1972).

Frigatebirds may prey on eggs and nestlings of other seabirds (Hill & Dunn 2004) and even take eggs or young of their own species (Nelson 1975), but this kind of nest failure is more characteristic of large and frequently disturbed colonies (del Hoyo *et al.* 1992).

The fact that broken eggs or egg remains were rarely found in the nesting areas could be related to the location of nest-sites. On Baluarte, nesting occurred on an old ship wreck, which could have been exposed to wave action during periods of high swell. Since rough seas are frequent in the archipelago from December to June, the only egg reported on this islet was probably washed away. On Curral Velho, nests were always located very close to the edge of the cliff and eggs could have been easily pushed off. During the 2005-2006 season, a broken egg and egg-shell remains were found on the two piles of rock that we had erected to prevent loss of eggs and nestlings.

Hatching failure appears to be related to infertility. Hatching success varied enormously across the 58 bird species examined by Morrow *et al.* (2002), ranging from 61-100%, with a mean of 12% of eggs failing to hatch, and across the 99 bird species examined by Spottiswoode & Møller (2004), with an average of 89.1%.

In four of the seven breeding seasons, an egg was incubated for a period of time that extended the normal incubation period of about 50 days reported for the species (Diamond 1973). We suspect that the fact that birds occupied nest 1 during three consecutive visits in the 2004-2005 season indicated the presence of an egg. It is also noteworthy that an egg was incubated for more than six months during the 2001-2002 season, until it was removed by us. This egg did not show signs of embryo development. During the 2003-2004 season, there was another egg at nest 1 for at least three months. Finally, an egg found broken on nest 1 during the 2005-2006 season did not show evidence of an embryo either.

Infertility and hatching failure in the small Cape Verde population may be due to genetic similarity and ageing. Severe bottlenecks reduce genetic diversity and increase inbreeding as individuals are forced to mate with close relatives (Briskie & Mackintosh 2004). Bird populations with high genetic

similarity often experience increased hatching failure due to infertility or embryo mortality (Spottiswoode & Møller 2004). Negative fitness effects often occur in isolated populations, such as those on islands (Ralls *et al.* 1979, Keller *et al.* 1994, Slate *et al.* 2000).

Nelson (1975) estimated life expectancy in frigatebirds to be 25.6 years, although some individuals probably live up to 40-50 years. Ageing may affect reproductive performance of long-lived seabirds. Anderson & Apanius (2003) found evidence for declining reproductive performance before age 20 in Nazca Booby *Sula granti*, in which both males and females showed age related declines in hatching and rearing success.

**Conservation** Seabirds are protected by law (Decree-law No.7/2000) in the Cape Verde Islands. Similarly, the most important seabird breeding sites in the archipelago are protected under the law for natural protected areas (Decree-law No.3/2003). According to this legislation, both islets, Baluarte and Curral Velho, were declared Integral Reserves. Access to these islets is restricted to scientific purposes and requires a special permit. Furthermore, in 2005, Cape Verde ratified the Ramsar Convention and the area of Curral Velho, including the islet became one of the first three Ramsar sites in the country. However, despite some improvements in the environmental legislation and the adherence to international treaties to protect Cape Verde biodiversity during recent years, large numbers of seabirds and sea turtles continue to be illegally harvested. Law enforcement and public awareness are deficient and there still exists a considerable degree of permissiveness among the environmental authorities.

The Magnificent Frigatebird is listed as critically endangered in the First Red List of Cape Verde (Hazevoet 1996). Long-term overexploitation ever since the archipelago was first colonized in the mid-15th century is likely the key factor behind the decline in population numbers and shrinking of the breeding range of Cape Verde's seabirds, particularly shearwaters, boobies, tropicbirds and frigatebirds. Reproductive failure, either resulting from genetic (inbreeding) or demographic imbalances (bottlenecks and ageing), are considered to have brought the frigatebird population on the verge of extinction. Intrinsic traits of frigatebird biology, such as very low productivity (due to female biennial breeding cycle, production of only one chick and frequent reproductive failure) and the lengthy period needed for birds to reach sexual maturity, combined with very low population numbers, mean that the Cape Verde frigatebird population is unlikely to be able of recovering on its own.

In conclusion, we do not think that this emblematic species of the Cape Verde Islands will manage to survive much longer. Basic conservation measures, such as population monitoring, habitat protection and a community-

based education programme, which may still help to preserve other threatened species in the archipelago, will likely come too late for the frigatebirds.

### ACKNOWLEDGEMENTS

Many thanks to José Geraldo Évora ('Zinho'), Rui David Ferreira Silva Nascimento ('Davidin') and Julião Silva Lima ('Djudja') for their help in surveying the islets. We would also like to thank DGA, INIDA and WWF-Cape Verde for their continuing interest and support. We are most grateful to Luís Palma (Faro) for reviewing earlier drafts of this paper and making many useful suggestions towards the improvement of it.

### BEPERKT BROEDHABITAT EN FALEN VAN REPRODUCTIE BIJ AMERIKAANSE FREGATVOGELS *FREGATA MAGNIFICENS* IN DE KAAPVERDISCHE EILANDEN

*De eilandjes Baluarte en Curral Velho, voor de kust van het eiland Boavista in de Kaapverdische Eilanden, zijn de enige broedplaatsen van de Amerikaanse Fregatvogel Fregata magnificens in de West Palearctis. Deze Oost-Atlantische relictpopulatie werd van de zomer 1999 t/m mei 2006 gemonitord. De meeste (inventarisatie)bezoeken werden in het broedseizoen gebracht, d.w.z. van november tot juni. Gedurende de laatste zeven achtereenvolgende broedseizoenen was het reproductiesucces nihil. Mogelijke oorzaken van mislukken van legsels zijn: 1) verlies van eieren tijdens de broedtijd; 2) niet uitkomen van eieren. De meest aannemelijke oorzaken hiervoor worden besproken. Vervolging en verstoring door mensen, een beperkt oppervlak aan broedhabitat, de geïsoleerde ligging en het uitblijven van broedsucces hebben de populatie op de rand van uitsterven gebracht. De overgebleven populatie, waarschijnlijk bestaand uit 4-5 adulte individuen (2 vrouwtjes ene 2-3 mannetjes), kan waarschijnlijk niet zelfstandig overleven.*

### REFERENCES

- Anderson D.J. & Apanius V. 2003. Actuarial and reproductive senescence in a long-lived seabird: preliminary evidence. *Experimental Gerontology* 38: 757-760.
- Austin J.J., White R.M.G. & Ovenden J.R. 1994. Population-genetic-structure of a philopatric, colonially nesting seabird, the short-tailed shearwater (*Puffinus tenuirostris*). *Auk* 111: 10-79.
- Bannerman D.A. & Bannerman W.M. 1968. History of the birds of the Cape Verde Islands. *Birds of the Atlantic Islands*, Vol. 4. Oliver & Boyd, Edinburgh.
- Bried J. & Jouventin P. 2002. Site and mate choice in seabirds: an evolutionary approach. Pp. 263-305 in: E.A. Schreiber & J. Burger (eds.), *Biology of Marine Birds*. CRC Press, Boca Raton, FL.
- Briskie J.V. & Mackintosh M. 2004. Hatching failure increases with severity of population bottleneck in birds. *Proceedings of the National Academy of Science USA* 101: 558-561.
- Carmona R., Guzmán J. & Elorduy J.F. 1995. Hatching growth and mortality of Magnificent Frigatebird chicks in southern Baja California. *Wilson Bulletin* 107: 328-337.
- Colin D. & Geiregat N. 2003. Trip Report: Cape Verde Islands, 05-21 April 2003. [www.birdtours.co.uk](http://www.birdtours.co.uk)
- Cramp S. & Simmons K.E.L. 1977. *The Birds of the Western Palearctic*, Vol. 1. Oxford University Press.
- Davis L. 1982. Timing of nest relief and its effect on breeding success in Adélie penguins (*Pygoscelis adeliae*). *Condor* 81: 178-183.

- Dearborn D.C. 2001. Body condition and retaliation in the parental effort decisions of incubating Great Frigatebirds (*Fregata minor*). Behavioral Ecology 12: 200-206.
- del Hoyo J., Elliot A. & Sargatal J. 1992. Handbook of the Birds of the World, Vol 1. Lynx Editions, Barcelona.
- de Naurais R. 1969. Notes brèves sur l'avifaune de l'archipel du Cap Vert. Faunistique, endémisme, écologie. Bulletin Institut Fondamental d'Afrique Noire (Ser. A) 31: 143-218.
- Diamond A.W. 1972. Sexual dimorphism in breeding cycles and unequal sex ratio in Magnificent Frigatebird. Ibis 114: 394-398.
- Diamond A.W. 1973. Note on the breeding biology and behavior of the Magnificent Frigatebird. Condor 75: 200-209.
- Diamond A.W. 1975. Biology and behaviour of Frigatebirds spp. on Aldabra Atoll. Ibis 117: 302-323.
- Durand M.L. 1992. Dimorfismo sexual en la conducta de reproducción y la deserción del macho en la *Fregata magnificens* en la isla Isabel, Nayarit. Unpublished BSc. Thesis. Facultad de Ciencias UNAM México.
- Erickstad K.E., Asheim M., Fauchald P. & Tveraa T. 1997. Adjustment of parental effort in the Puffin: the roles of adult body condition and chick size. Behavioral Ecology and Sociobiology 40: 95-100.
- Fisher H.I. 1976. Some dynamics of a breeding colony of Laysan albatrosses. Wilson Bulletin 88: 121-142.
- Gibson-Hill C.A. 1947. Notes on the birds of Christmas Island. Bulletin of the Raffles Museum 18: 87-165.
- Harrison P. 1983. Seabirds: an identification guide. Houghton Mifflin, Boston.
- Hazevoet C.J. 1994. Status and conservation of seabirds in the Cape Verde Islands. Pp. 279-286 in: D.N. Nettleship, J. Burger & M. Gochfeld (eds.), Seabirds on islands: threats, case studies and action plans. BirdLife Conservation Series 1.
- Hazevoet C.J. 1995. The Birds of the Cape Verde Islands. B.O.U. Check-list 13. British Ornithologists' Union, Tring.
- Hazevoet C.J. 1996. Lista Vermelha para as aves que nidificam em Cabo Verde. Pp. 127-135 in: T. Leyens & W. Lobin (eds.), Primeira Lista Vermelha de Cabo Verde. Courier Forschungsinstitut Senckenberg 193.
- Hill R. & Dunn A. 2004. National Recovery Plan for the Christmas Island Frigatebird *Fregata andrewsi*. Commonwealth of Australia, Canberra.
- Keller L.F., Arcese P., Smith J.N.M., Hochachka W.M. & Stearns S.C. 1994. Selection against inbred Song sparrows during a natural population bottleneck. Nature 372: 356-357.
- Monaghan P., Uttley J.D. & Burns M.D. 1992. Effect of changes in food availability on reproductive effort in Arctic terns, *Sterna paradisaea*. Ardea 80: 71-81.
- Morrow E.H., Arnqvist G. & Pitcher T.E. 2002. The evolution of infertility: does hatching rate in birds coevolve with female polyandry? Journal of Evolutionary Biology 15: 702-709.
- Nelson J.B. 1967. Etho-ecological adaptations in the Great Frigate Bird. Nature 214-218.
- Nelson J.B. 1975. The breeding biology of frigatebirds: a comparative review. Living Bird 14: 113-155.
- Noeske A. & Pflütze S. 1994. The Cape Verde Islands: Tropical birding in the Western Palearctic. Birding World 7: 152-160.
- Osorno J.L. 1996. Evolution of breeding behavior in the Magnificent Frigatebird: copulatory pattern and parental investment. Unpublished Ph.D. Dissertation, University of Florida, Gainesville, FL., USA.
- 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.
- Ralls K., Brugger K. & Ballou J. 1979. Inbreeding and juvenile mortality in small populations of ungulates. Science 206: 1101-1103.

- Reville B.J. 1988. Effects of spacing and synchrony on breeding success in the Great Frigatebird (*Fregata minor*). *Auk* 105: 252-259.
- Reville B.J. 1991. Nest spacing and breeding success in the Lesser Frigatebird (*Fregata ariel*). *Condor* 93: 555-562.
- Schørring S. 2001. Ecologically determined natal philopatry within a colony of great cormorants. *Behavioral Ecology* 12: 287-294.
- Schreiber R. W. & Ashmole N.P. 1970. Sea-bird seasons on Christmas Islands, Pacific Ocean. *Ibis* 112: 363-394.
- Schreiber E.A. & Schreiber R.W. 1993. Red-tailed tropicbird (*Phaethon rubricauda*). *The Birds of North America* 43. Academy of Natural Sciences, Philadelphia & American Ornithologists' Union, Washington DC.
- Sibley C.G. & Monroe B.L. 1990. *Distribution and taxonomy of Birds of the World*. Yale University Press, New Haven.
- Slate J., Kruuk L.E.B., Marshall T.C., Pemberton J.M. & Clutton-Brock T.H. 2000. Inbreeding depression influences lifetime breeding success in a wild population of red deer (*Cervus elephas*). *Proceedings of the Royal Society of London B* 267: 1657-1662.
- Spottiswoode C. & Møller A.P. 2004. Genetic similarity and hatching success in birds. *Proceedings of the Royal Society of London B* 271: 267-272.
- Stonehouse B & Stonehouse S. 1963. The Frigatebird *Fregata aquila* on Ascension Island. *Ibis* 103b: 409-422.
- Trivelpiece W.Z. & Ferraris J.D. 1987. Notes on the behavioural ecology of the Magnificent Frigatebird *Fregata magnificens*. *Ibis* 129: 168-174.
- Weimerskirch H. 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* 102: 37-43.
- Weimerskirch H., Chastel O., Barbraud C. & Tostain O. 2003. Frigatebirds ride high on thermals. *Nature* 421: 333-334.
- Weimerskirch H., Le Corre M., Marsac F., Barbraud C., Tostain O. & Chastel, O. 2006. Postbreeding movements of frigatebirds tracked with satellite telemetry. *Condor* 108: 220-225.

**APPENDIX: SUMMARY OF THE MAIN EVENTS OBSERVED PER SEASON**  
**SAMENVATTING VAN DE BELANGRIJKSTE WAARNEMINGEN PER SEIZOEN**

**SEASON: 1999-2000**

**Curral Velho** 6 & 17 August, 10 September, 21 October, 26 November, 7 December, 12 January, 9 February, 3 March, 12 April & 2 June.

**Baluarte** 24 & 30 June, 26 July, 25 August, 13 September, 9 October, 13 December, 13 January, 10 February, 7 March, 13 April & 1 June.

**Nesting** Frigatebirds nesting on Curral Velho. Two nests: Nest 1 with an egg incubated by a female on 7 December; occupied by a male on 12 January; and without egg and deserted on 9 February. Nest 2 had a male incubating an egg on 12 January; occupied by a male on 9 February and by a female on 3 March and 12 April; deserted on 2 June.

**Sightings** Both islets surveyed every month to establish breeding period and estimate population numbers. Frigatebirds sighted at Curral Velho on all visits except October and November. Three males and two females observed on 12 April. Five birds were observed on Baluarte in June 1999.

## SEASON: 2000-2001

**Curral Velho** 12 January, 11 April & 17 May. Logistics hindered a monthly survey, and the islet was not visited in February and March.

**Baluarte** Not surveyed due to logistic problems. Breeding reported on Curral Velho in January.

**Nesting** The birds used the same two nests reported in the previous season. Nest 1 with an incubating female on 12 January; still with a female in April; and deserted on 17 May. An egg out of Nest 2, which was occupied by a male, on 11 April. Nest deserted in May.

**Sightings** The observation of three individuals, two males and one female, in April was the most notable sighting of this season.

## SEASON: 2001-2002

**Curral Velho** 2 December, 27 March, 2 May & 10 June.

**Baluarte** Only surveyed on 25 December to check for synchronous nesting activity on both islets. Egg-laying on Curral Velho had already been reported in December.

**Nesting** Frigatebirds re-used the same two nests on Curral Velho. An incubating female was reported on Nest 1 in December. Nest occupied by a female in March and by a male in May. The egg, still being incubated by a female, was removed on 10 June. Nest 2 occupied by a male in December and March; by an incubating female in May; and deserted in June.

**Sightings** Four individuals, two males and two females, sighted in December and May. No birds reported on Baluarte in the only survey on 25 December.

## SEASON: 2002-2003

**Curral Velho** 31 January & 28 February. Visits stopped once nesting activity was reported on Baluarte.

**Baluarte** 10 March, 6 April, 4 May & 31 July. Not surveyed early in the season, because of logistic constraints. Surveyed by Colin & Geiregat (2003) in April.

**Nesting** Only season in which nesting activity took place on Baluarte. Nest site on the remains of a shipwreck, situated on the south shore of the islet. A male perched on a nest was reported in March. Two females occupying two nests were reported on 6 April 2003 by Colin & Geiregat (2003). An incubating female was observed in May. Nest site deserted in July.

**Sightings** Apart from a male at the nest, another two males near the nesting site and a female flying over the islet were sighted on 10 March 2003. Two females and four males (two of which in breeding condition) were sighted by Colin & Geiregat (2003) in April. An incubating female and a male flying over the islet were reported in May. A single male flying over Baluarte was reported in July. No sightings on Curral Velho were made during visits in January and February.

## SEASON: 2003-2004

**Curral Velho** 17 November, 8 December, 10 January, 11 February, 24 March, 13 April, 25 May, 19 June & 30 July.

**Baluarte** 6 December, 27 January, 19 February, 2 April & 23 June.

**Nesting** Two new nests in the usual nesting area on Curral Velho. Nest 1 was occupied by a female on 8 December, 3 and 10 January. A male incubating an egg was reported in February. Egg was still being incubated by a female in March, a male in April and again by a female in May. Egg shell remains were found in July. Nest 2 was occupied by a male in December and by a female in January, but no egg was seen; nest unoccupied in February and re-occupied by a female in March; deserted from April onwards.

**Sightings** Two males and two females was the largest number of birds sighted during the season on Curral Velho. No frigatebirds were observed in June and July. A male in breeding condition on 23 June was the only sighting on Baluarte.

SEASON: 2004-2005

**Curral Velho** 12 January, 12 February, 24 March, 22 April, 14 May & 16 June.

**Baluarte** 25 January & 21 February.

**Nesting** Frigatebirds utilized the same two nests as in the previous season. Nest 1 was occupied by a female in January and February and by a female in March, deserted from April onwards. Nest 2 had a non-incubating female in February, an egg incubated by a male in March, and was deserted on 22 April 2005.

**Sightings** A dead male was found on Baluarte on 25 January. This male, identified by a green piece of cord tied to the left leg, was last sighted alive on 13 April 2004 on Curral Velho.

SEASON: 2005-2006

**Curral Velho** 14 October, 11 November, 20 December, 22 January, 27 February, 24 March, 20 April & 22 May.

**Baluarte** 3 January, 4 February, 23 March, 24 April & 25 May.

**Nesting** Nesting on the two piles of rocks arranged in the 2002-2003 season to prevent the accidental loss of the egg. Nest 1 had an egg on 11 November. This egg was found broken in December. Nest 2 had an incubating male on 20 December, an egg incubated by a female in January, and egg shell remains on 27 February.

**Sightings** Two males and two females sighted on 11 November. Four frigatebirds also reported in April: a female perched on a nest, a male and another female flying over Curral Velho, and an immature bird overflying the area. No birds sighted on Curral Velho in May. No records of frigatebirds during any of the five visits to Baluarte conducted in the season.