

FACTORS AFFECTING THE BREEDING SUCCESS OF ARCTIC TERNS *STERNA PARADISAEA* IN A COLONY AT KALDBAKSBOTNUR, FAROE ISLANDS

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Schreiber, J. & Kissling, W.D. 2005. Factors affecting the breeding success of Arctic Terns *Sterna paradisaea* in a colony at Kaldbaksbotnur, Faroe Islands. *Atlantic Seabirds* 7(3): 97-105. *Food shortage and predation are the main factors limiting the breeding success of many colonial seabirds. The aim of this study was to examine whether they influence breeding success of Arctic Terns Sterna paradisaea in a colony of 99 breeding pairs at Kaldbaksbotnur on the island of Streymoy, Faroe Islands. In 2003, we investigated clutch size, hatching success, food provisioning to chicks, kleptoparasitism, and predation, and the number of fledged chicks. Clutch size was on average 1.65 (± 0.48) eggs/clutch with a hatching success of 100%. Food provisioning rates were low with 0.47 (± 0.18) feeds per nest per hour. Most prey items were small (c. 32 mm long), and terns showed high rates of intraspecific kleptoparasitism. Attacks by avian predators were occasionally observed, mainly by Herring Gulls *Larus argentatus*, but were unsuccessful in all observed cases. Counts of fledged chicks indicated average breeding productivity of 0.22 chicks per pair. Our results suggest that breeding success in this colony was mainly affected by food shortage, possibly limited sandeel *Ammodytes* spp. availability. Predation appears to be less important, but could occur at a low rate. The results are consistent with recent evidence showing that seabirds that feed on sandeels currently have limited breeding success in the North Atlantic region.*

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INTRODUCTION

As a circumpolar breeding species, Arctic Terns *Sterna paradisaea* are widespread in the North Atlantic region (del Hoyo *et al.* 1996), including the Faroe Islands. In 1981, the Faroese population of Arctic Terns was estimated to be 11,800 pairs (Bengtson & Bloch 1983). In recent years, a marked decline in the population was assumed because the numbers and sizes of colonies seemed to have decreased (B. Olsen, *pers. comm.* 2003). However, since the investigations by Bengtson & Bloch (1983) no detailed studies on Arctic Terns have been conducted on the Faroe Islands, and the factors influencing Arctic

Tern breeding success and population trends at this locality are not known. Two main factors are commonly reported to influence the breeding success of colonial seabirds. Firstly, major breeding failures are often caused by food shortage (Croxall *et al.* 1999; Mavor *et al.* 2004, 2005), and this has been confirmed for Arctic Terns in particular (Monaghan *et al.* 1992; Suddaby & Ratcliffe 1997). Secondly, predation is known to be a major factor causing declines in seabird numbers including Arctic Terns (Becker 1995; Whittham & Leonard 1999, 2000; Nordström *et al.* 2004).

The aim of this study was to investigate factors influencing breeding success of Arctic Terns in one colony on the Faroe Islands. We examined whether Arctic Tern breeding success at this site is affected by predation and/or food availability. We thus determined clutch size and hatching success, observed food provisioning to chicks, kleptoparasitism, and predation attacks, and finally counted fledged chicks. The results may help to evaluating potential reasons for the decline in Faroese Arctic Tern numbers.

METHODS

Arctic Terns were studied in 2003 at one colony on the Faroe Islands - Kaldbakbotnur (62°04' N; 6°55' W) on the main island of Streymoy, 13 km north-west of the capital Tórshavn. The study site was visited at least every two days by one or two observers. Observations on food provisioning, kleptoparasitism, and predation were made with binoculars and a spotting scope from a nearby hill about 45 m from the colony centre. During the incubation period, nests within the colony were visited every 4-5 days to determine clutch sizes, hatching success (i.e. the percentage of nests producing at least one chick), and chick numbers. To minimize disturbance, 30 intensive study nests in different parts of the colony were selected for frequent checks during the whole season. Twenty of these were marked with numbers on wooden sticks for detailed observations from outside the colony. Once hatching had started, the 30 clutches were checked every two days. No visits were made during unfavourable weather conditions. The number of eggs or chicks was registered during each visit as well as any signs of imminent hatching.

To investigate food provisioning to chicks and kleptoparasitism, terns were observed at 11 of the 30 study nests. Observations were made in series within four days between 0400 hrs and 2200 hrs GMT over several hours at different times of day. However, this was often difficult because of poor weather conditions, fog and heavy rain rendering fieldwork impossible. Therefore data from incomplete observation series were used only to calculate the rate of kleptoparasitism. For calculations of the food provisioning rate only one complete observation series could be used (15-18 July) when five nests

were monitored continuously for 14 hours. Kleptoparasitism was investigated by recording attacks from other Arctic Terns, their duration, and the success or failure of the food provisioning event. Food provisioning rate was calculated as the number of prey items delivered to the chick per nest per hour (nests only contained one chick). Prey size was estimated in adult tern bill lengths whenever visible. In most cases, prey species were not identified.

Predation was assessed at two levels. Predation attacks from flying predators were observed from outside the colony on each visit to the study site (a total of 61 observation hours). In addition, the disappearance of eggs and/or chicks from our 30 intensive study nests was taken to indicate predation by avian and/or mammalian predators. For predator observations from outside the colony, the following parameters were recorded: time of predation event, number and species of predator, reaction of the terns, and success/failure of the attack.

In order to estimate breeding productivity of this colony, seven counts of large and fledged chicks were made between 23 July and 5 August. Counts were facilitated by adults leading their chicks to a nearby stream, where they were easily visible. The maximum number of large and fledged chicks was divided by the number of breeding (i.e. egg laying) pairs, and this value was taken as an estimate of the breeding productivity per pair in this colony (see Walsh *et al.* 1995).

RESULTS

Clutch size and hatching A total of 99 breeding pairs was recorded; 64 were two-egg clutches (65%) and 35 one-egg clutches (35%). An overall, average clutch size of 1.65 (\pm 0.48) eggs per clutch was estimated. The 30 intensive study nests contained a total of 47 eggs, and thus the mean clutch size (1.57 \pm 0.5 eggs/clutch) of this sample was relatively similar to the overall estimate. Two eggs or chicks disappeared from the clutches and were thus considered to be depredated, and three eggs (6%) were given up. Thus, a total of 42 chicks hatched from these 30 clutches. All of the lost eggs were part of a two-egg clutch in which the other chick hatched. Thus, none of the clutches was lost completely during incubation resulting in hatching success of 100%. The hatching peak was reached between 4 and 7 July.

Food provisioning Thirty-three successful feeds were observed at the five selected nests during the 14 hours observation period, resulting in a food provisioning rate of 0.47 (\pm 0.18) feeds per nest per hour. In most cases (39%), the terns fed small fish with only one bill-length in size; other prey sizes were less frequent (Figure 1). Given a bill-length of 32 mm (Glutz von Blotzheim &

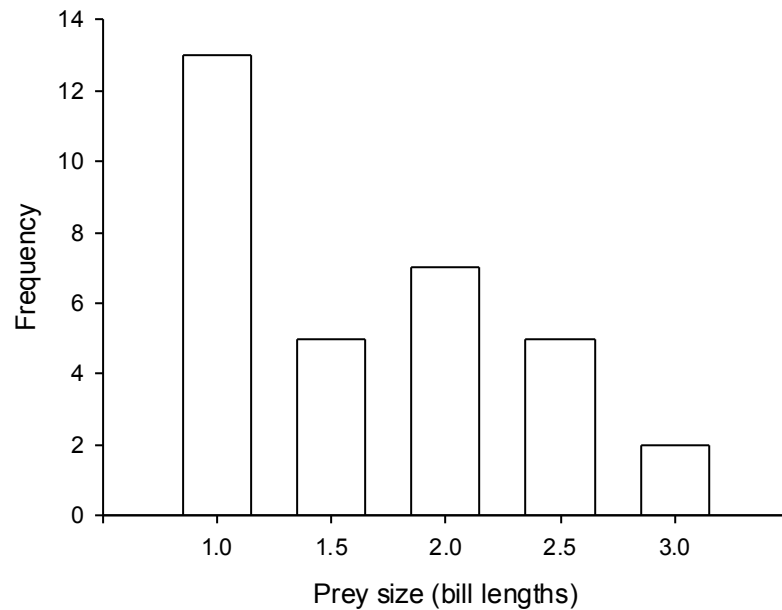


Figure 1. Frequency distribution of prey sizes ($n = 32$) fed by Arctic Terns at Kaldbakshotmur, Faroe Islands. Prey size was estimated in adult bill lengths (c. 32 mm).

Figuur 1. Frequentieverdeling van prooigroottes ($n = 32$) waarmee Noordse Sterns hun jongen voerden in Kaldbakshotmur, Færøer. Prooigrootte werd geschat in snavellengtes van de adulte vogel (ca 32 mm).

Bauer 1982), a mean prey size of $53 (\pm 21)$ mm (median = 48; $n = 32$) may be estimated. The food spectrum seemed to consist almost exclusively of fish species. Most prey was probably sandeel *Ammodytes* spp., but identification was difficult in most cases.

Kleptoparasitism A total of 96 feeds was recorded during the whole observation period, of which 47 (49%) were disrupted by intraspecific kleptoparasitism. Most kleptoparasitic attacks (47%) lasted up to 4 minutes, but some (11%) lasted more than 8 minutes (Figure 2). One tern was harassed for more than 20 minutes, having numerous attempts to feed its chick. Despite the frequent kleptoparasitic attacks, only 26% of food provisioning attempts failed.

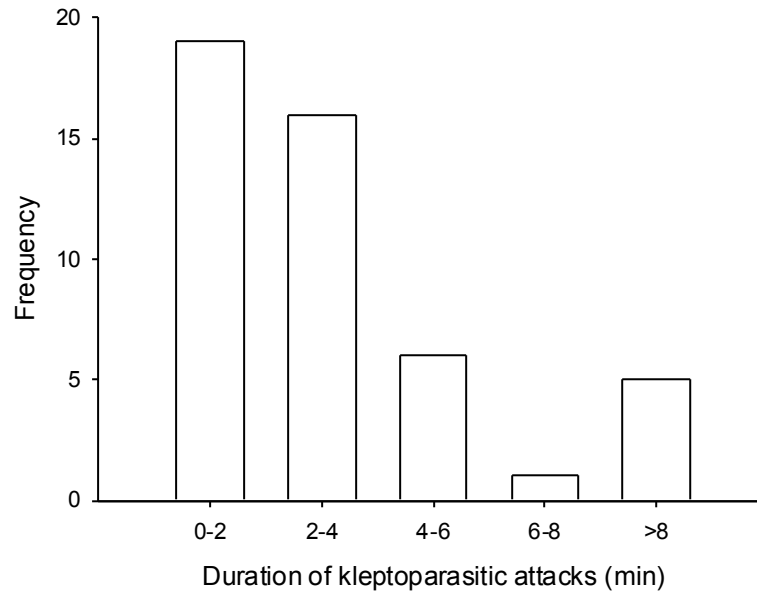


Figure 2. Frequency distribution of duration of kleptoparasitic attacks ($n = 47$) in a colony of Arctic Terns at Kaldbakshotmur, Faroe Islands.

Figuur 2. Frequentieverdeling van de duur van kleptoparasitaire aanvallen ($n = 47$) in een kolonie Noordse Sterns in Kaldbakshotmur, Faröer.

The failures were due to prey being swallowed or dropped by the attacked adults or taken away by the kleptoparasites.

Predation During 61 hours of monitoring flying predators at the colony, only 26 events involving 29 individual predators were recorded. Most of the flying predators (58%) were Herring Gulls *Larus argentatus*. Other potential predators included Great Black-backed Gull *L. marinus* (11%), Black-headed Gull *L. ridibundus* (11%), Black-legged Kittiwake *Rissa tridactyla* (8%), Arctic Skua *Stercorarius parasiticus* (8%) and Merlin *Falco columbarius* (4%). In 65% of the cases, the terns attacked the potential predators. Even harmless species were attacked, for instance Whimbrels *Numenius phaeopus* and a White-winged Black Tern *Chlidonias leucopterus*. However, we observed only one direct attempt (4%) to rob eggs or chicks when an Arctic Skua tried to land in the colony, but this was unsuccessful due to sustained attacks by the terns. Thus, no

losses of eggs or chicks could be witnessed directly during observations and only two eggs or newly hatched chicks disappeared during our frequent clutch checks (see above).

Breeding productivity Between 2 and 4 August, a maximum number of 22 fledged chicks was counted. Based on this number, overall breeding productivity for this colony was estimated to be 0.22 chicks per pair.

DISCUSSION

The estimated breeding productivity of 0.22 chicks per pair is a relatively low value compared with other Arctic Tern colonies (Mavor *et al.* 2004). Annual productivity of Arctic Terns in the British Isles in the years 2002 and 2003 ranged from complete failure (e.g. Shetland) to 1.44 chicks per pair (Wales), with an average of approximately 0.44 chicks per pair (Mavor *et al.* 2004). Long-term mean values (1986-2002) at the same sites ranged from 0.10 chicks per pair (Scotland) to 1.09 chicks per pair (Wales), with an average value of 0.43 chicks per pair (Mavor *et al.* 2004). Our method used to estimate the reproductive success is not the most accurate as some chicks might have been overlooked in high grass. However, together with the other results of our study (see below) it suggests that breeding productivity in this colony was strongly limited. Since breeding and foraging ecology of Arctic Terns seems to vary widely in space and time we recommend more detailed and long term investigation at Faroese tern colonies aimed at assessing population trends and annual productivity.

Productivity of Arctic Terns nesting at Kaldbaksbotnur seemed to be little affected by predation since no losses of eggs or chicks could be directly assigned to avian predators during 61 hours of observation, and only two eggs or newly hatched chicks disappeared from our monitored clutches. The reason for such low avian predation pressure might be that breeding predators in the surroundings of the tern colony were largely absent. Becker (1995) studied gull predation on Common Terns *S. hirundo* in a colony adjacent to a Herring Gull colony of 10,500 pairs in the German Wadden Sea, and reported chick losses of 44 % to 94 % due to gull predation. He suggested that most of these gulls did not specialize in robbing chicks, but took them as supplementary food. Predation rates might therefore be strongly influenced by predator breeding densities adjacent to tern colonies. We did not directly investigate potential effects of mammalian predators (most likely Brown Rats *Rattus norvegicus*; B. Olsen, *pers. comm.*) on Arctic Tern productivity. However, since only two eggs or newly hatched chicks disappeared from our monitored clutches, we would expect mammalian predation at this site also to be low.

Several findings from this study suggest that the relatively low tern productivity was probably caused mainly by food shortage. The food provisioning rate of 0.47 (± 0.18) feeds per nest per hour at our Faroese tern colony is clearly lower than comparable food provisioning rates of 0.71 and 1.37 trips per nest per hour in an Arctic Tern colony in Shetland (Monaghan *et al.* 1992). Most prey items delivered to chicks in our colony were small with a mean size of 53 (± 21) mm. Monaghan *et al.* (1989) reported a high proportion of very small sandeels in a colony where breeding failed completely, and concluded that intermediate sized sandeels are a prerequisite for successful reproduction. The high frequency of intraspecific kleptoparasitism also suggests that food availability was limited. Ludwigs (1998) found that high intraspecific kleptoparasitism in a colony of Common Terns in the German Wadden Sea was caused by very poor food supply. He reported attacks on 15 % of food provisioning attempts, 75 % of which ended successfully for the kleptoparasites. Our observations on the Faroe Islands differed because attacks occurred more often (49%) but were less successful (26%). This suggests high kleptoparasitism pressure due to limited food availability. Overall, evidence for food shortage limiting breeding productivity was thus indicated by low food provisioning rates, relatively small prey items, and frequent intraspecific kleptoparasitism. The average clutch size of 1.65 (± 0.48) eggs per clutch is similar to that in other studies, e.g. 1.76 to 1.94 eggs per clutch in the British Isles (Monaghan *et al.* 1989, 1992), and 1.5 eggs per clutch in the German Wadden Sea (Frick & Becker 1995).

A major component of Arctic Tern diet in the North Atlantic is sandeels (Monaghan *et al.* 1989, 1992; Suddaby & Ratcliffe 1997), and adult terns generally feed their chicks on sandeels of the current year, while the adults themselves mostly feed on sandeels of the previous year (Monaghan *et al.* 1992). Several Arctic Tern populations in Shetland, west, and north-east Scotland exhibited large declines between 2002 and 2003, which were attributed to low availability of sandeels (Mavor *et al.* 2004). Low sandeel availability appears to continue to be a severe problem for many seabirds in the North Sea, and probably accounted for an almost complete breeding failure of Arctic Terns in Orkney, Shetland, and NE and SE Scotland the year following our study (Mavor *et al.* 2005). Earlier dramatic declines in breeding numbers of Arctic Terns in Shetland between 1984 and 1988 were also attributed to a decline in sandeel populations (Monaghan *et al.* 1992). The recent decrease in numbers and sizes of Arctic Tern colonies on the Faroe Islands might therefore be most likely explained by limited sandeel availability. Since no sandeel fishery exists around the Faroe Islands, other factors such as demographic or environmentally induced changes in sandeel survival and abundance might be responsible for

potentially low sandeel availability in this region (Fisheries Research Services 2003).

We conclude that breeding productivity of Arctic Terns in the Kaldbaksbotnur colony was primarily affected by food shortage (possibly limited sandeel availability). This is consistent with recent evidence showing that seabirds that feed on sandeels currently have limited breeding success in the Northern Atlantic region (Mavor *et al.* 2004, 2005). In order to achieve deeper insights into the spatial and temporal variation of Arctic Tern productivity at the Faroe Islands, it would be desirable to investigate more sites, and to monitor colonies over a longer time period.

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FACTOREN DIE HET BROEDSUCCES BEPALEN VAN NOORDSE STERNS *STERNA PARADISAEA* IN KALDBAKSBOTNUR, FARÖER

*Voedselgebrek en predatie zijn de belangrijkste factoren die het broedsucces van vele kolonie-broedende zeevogels beperken. Het doel van dit onderzoek was te onderzoeken of deze factoren invloed hebben op het broedsucces van Noords Sterns *Sterna paradisaea* in een kolonie van 99 broedpaar in Kaldbaksbotnur op het eiland Streymoy, Farøer. In 2003 onderzochten we legselgrootte, uitkomstsucces, voederen van de kuikens, kleptoparasitisme, predatie en het aantal uitgevlogen jongen. De legselgrootte bedroeg gemiddeld 1.65 (± 0.48) ei/legsel met een uitkomstsucces van 100%. Voederfrequenties waren laag met 0.47 (± 0.18) voederbeurten per nest per uur. De meeste prooien waren klein (ca 32 mm lang). De sterns ondervonden een hoog aandeel van intraspecifiek kleptoparasitisme. Aanvallen door vogels werden soms waargenomen, met name door Zilvermeeuwen *Larus argentatus*, maar deze waren in alle waargenomen gevallen niet succesvol. Tellingen van uitgevlogen jongen wezen op een gemiddeld broedsucces van 0.22 kuiken per paar. Onze resultaten suggereren dat het broedsucces in deze kolonie grotendeels wordt beïnvloed door voedselgebrek, mogelijk door een beperkend aanbod zandspiering *Ammodytes* spp.. Predatie lijkt minder belangrijk, maar kan in een lage frequentie optreden. De resultaten zijn consistent met recente bevindingen dat zeevogels die op zandspiering foerageren, in de Noord-Atlantische regionen tegenwoordig een laag broedsucces hebben.*

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

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HAZEVOET³ & LUÍS FELIPE LÓPEZ JURADO^{1,2}.

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.*

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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

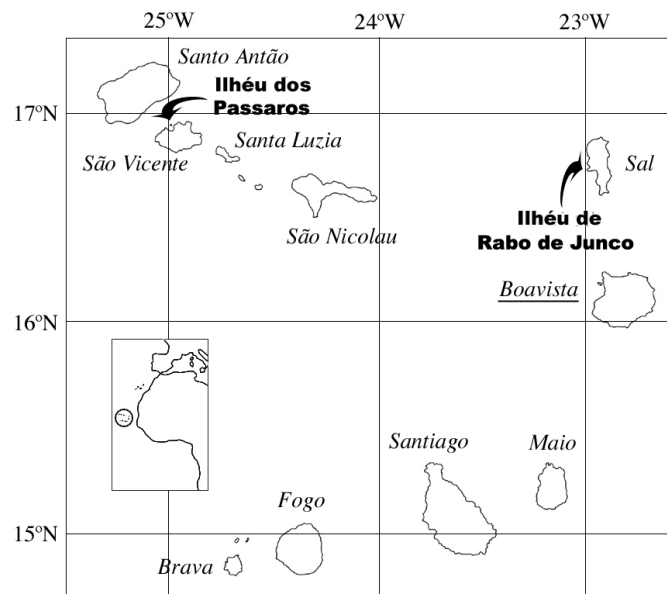


Figure 1. Map of the Cape Verde Islands.
 Figuur 1. Plattegrond van de Kaap Verdische Eilanden.

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.

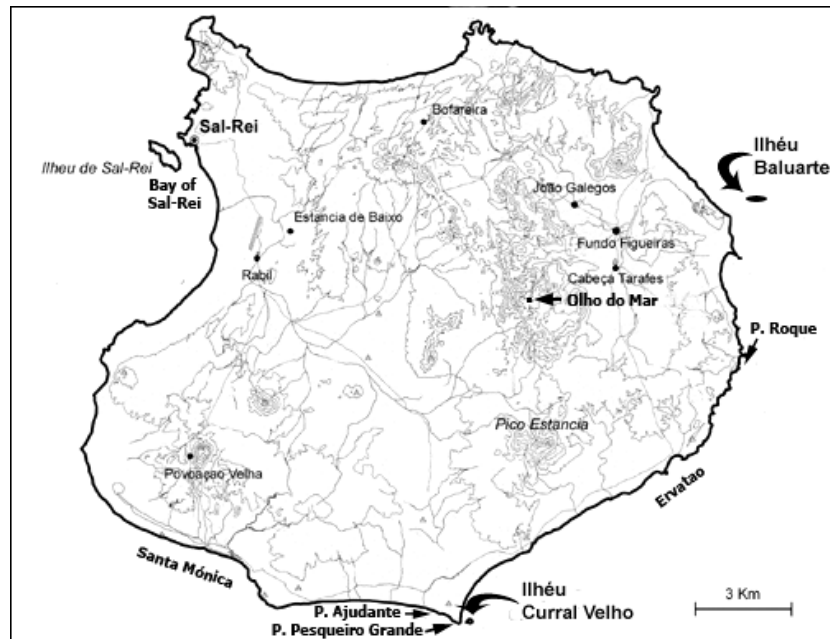


Figure 2. Map of Boavista, showing localities mentioned in the text.

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 km²) 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 km². 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.

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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.

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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.

LARGE NUMBERS OF CAPE VERDE
SHEARWATERS *Calonectris edwardsii* OFF
SANTO ANTÃO, CAPE VERDE ISLANDS,
IN JULY 2005

PETER VAN HORSSSEN¹

Horssen, P. van 2006. Large numbers of Cape Verde Shearwaters *Calonectris edwardsii* off Santo Antão, Cape Verde Islands, in July 2005. *Atlantic Seabirds* 7(3): 121-126. During systematic sea watching in the period 20–27 July 2005 at Ponta do Sol, Santo Antão, Cape Verde Islands, a total of 6653 Cape Verde Shearwaters *Calonectris edwardsii* were counted. Largest numbers were counted 2–2.5 hours before sunset. Main flight direction was east. Numbers of Cape Verde Shearwaters were low 1–1.5 hours after sunrise, with the main flight direction being west.

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INTRODUCTION

Breeding distribution of the Cape Verde Shearwater *Calonectris edwardsii* is confined to the Cape Verde Islands. In 1988-1993, the population was estimated at c. 10,000 pairs, with main breeding colonies situated on Branco, Raso and Brava, and smaller colonies on Santiago, São Nicolau, Boavista, and Sal (Hazevoet 1995, Hazevoet *et al.* 1996). Cape Verde Shearwater is listed as 'near threatened' on the IUCN Red List (Birdlife International 2005).

Cape Verde Shearwaters are absent from the breeding region from late November until late February (Hazevoet 1995). Birds arrive in the colonies from late February to early March, egg laying and incubation takes place in May-July, and young fledge from late September to November (Hazevoet 1995). Behaviour is poorly known, but many aspects are presumably as in Cory's Shearwater. Daily activity during the breeding period is also poorly known and very little numerical information is available from any moment in the life cycle of the Cape Verde Shearwater. This paper presents the results of systematic land based counts on Santo Antão during the period 20–27 July 2005.

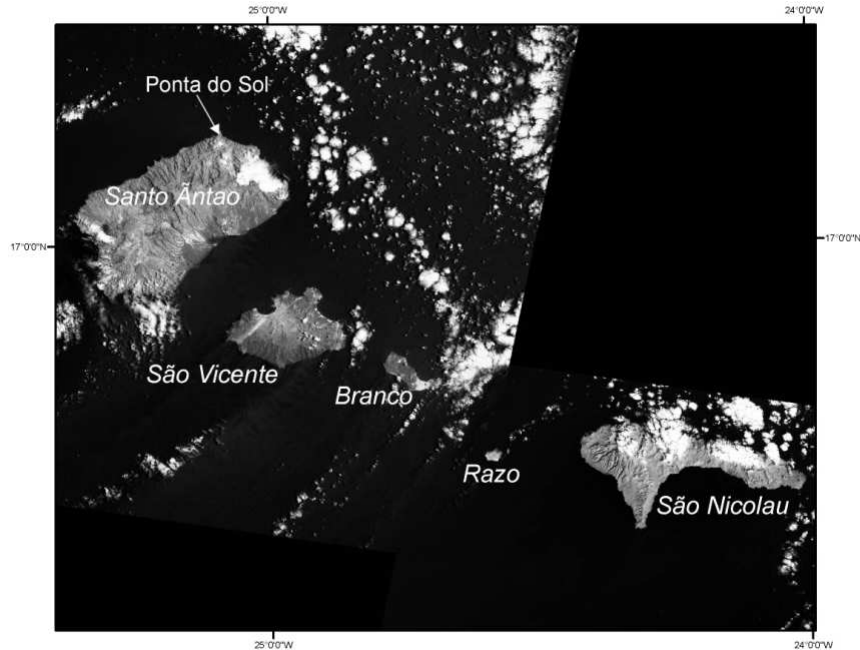


Figure 1. Location of Ponta do Sol, Santo Antão, Cape Verde Islands
 Figur 1. Ligging van Ponta do Sol, Santo Antão, Kaap Verdische Eilanden.

METHODS

Observations of passing Cape Verde Shearwaters were made from a vantage point at Ponta do Sol, Santo Antão ($17^{\circ}12'00''\text{N}$, $25^{\circ}05'23''\text{W}$). The observation point was located 500 m from the actual coastline at an altitude of c. 50 meters a.s.l. The village of Ponta do Sol is located on the northern coast of Santo Antão and constitutes the most northerly point of the Cape Verde Islands (Figure 1). Observations were made with 10x42 binoculars. All birds up to an estimated 750–1,500 m from the coastline were counted. Flight direction (either east or west) and behaviour (foraging, rafting, passing by) were noted. Nearly daily counts were made two hours after sunrise and three hours before sunset. Other hours of the day were subsequently sampled during the six day period, with 15 minute counts each hour (Table 1). Because of the banking behaviour in the northeast trade winds, birds flying east were more easily detected than birds flying west, who generally flew without banking.

Table 1. Periods counted, cloud cover, wind direction, wind force and visibility (F = fully counted; - = no wind or direction; empty fields indicate missing values).

Tabel 1. Teltijden, bewolking, windrichting, windkracht en zicht (f = volledig geteld; - = geen wind of richting; lege velden geven ontbrekende waarden aan).

Date	from	until	n 15 min periods	Total (hours)	cloud cover	wind direction	wind force	visibility
20-07	12:30	16:00	8	2,0				
	16:45	19:00	F	2,25	8/8	NO	3/4	<1 km
21-07	6:00	7:30	F	1,5	8/8	NO	2/3	<2km
	14:00	14:15	1	0,25				
	16:57	19:00	F	2,05	1/8	NO	5/6	
22-07	6:00	7:00	F	1	8/8	NO	1/2	
	16:43	19:30	F	2,75	6/8	NO	3/4	<2km
23-07	9:07	9:22	F	0,25				
	13:57	14:07	F	0,25				
	16:00	19:30	F	3,5	8/8	N	3/4	<5km
24-07	6:00	7:30	F	1,5	6/8 > 7/8	-	-	<1km
	8:40	8:55	F	0,25	7/8	-	-	<1km
	12:15	14:15	2	0,5	6/8;4/8	NO	3/2;3/4	<1km
	17:25	19:15	F	1,83	1/8	NO	4/5	<2,5km
25-07	6:00	7:00	F	1	7/8	NO	0/1	<1km
	13:45	14:35	2	0,5	8/8	NO	1/2	<1km
	15:00	19:00	F	4,0	3/8	NO	4/5	<1km
26-07	6:00	7:45	F	1,75	8/8	N	2/3	3km
	8:30	8:45	1	0,25	8/8	N	1/2	3km
	16:30	19:20	F	2,84	2/8 > 7/8	NO	2/3	5km
27-07	6:00	7:00	F	1,0	2/8	NNO	2/3	5km
	10:15	13:30	3	0,75	3/8	N;N:NO	2/3;3/4;3/4	5km

Of all passing birds 99% were Cape Verde Shearwaters. The light underwing and belly of Cape Verde Shearwaters made it easy to distinguish the species from the occasional passing Cape Verde Petrel *Pterodroma feae*. One afternoon was spent at the coastline to examine shearwaters passing by at close range (< 25 m). Based on bill structure and plumage colour all birds examined were Cape Verde Shearwaters. The occurrence of the closely related and rather similar looking Cory's Shearwater *C. borealis* and Scopoli's Shearwater *C. diomedea* in Cape Verde waters is confined to the winter months (Hazevoet 1995).

Table 2. Numbers of Cape Verde Shearwaters and hours per day counted at Ponta do Sol, Santo Antão, Cape Verde Islands.

Tabel 2. Aantallen Kaapverdise Pijlstormvogels en aantal per dag getelde uren op Ponta do Sol, Santo Antão, Kaap Verdise Eilanden.

Date	Numbers	Hours counted
20-7	211	4,25
21-7	324	3,80
22-7	904	3,75
23-7	1247	4,00
24-7	1345	4,08
25-7	533	5,50
26-7	2088	4,84
27-7	1	1,75
Total	6653	31,97

RESULTS

The daily number of Cape Verde Shearwaters counted varied from 211 to 2,088 birds (Table 2). Numbers counted during the first afternoon were approximately 10 % of those counted during the last afternoon. During the course of the afternoon, numbers of Cape Verde Shearwaters increased from c. 3.5 hours before sunset until dusk. The highest numbers, with a maximum of 152/15 min. period, occurred 1,5 hour before sunset (Figure 2). The main flight direction before sunset was east. The number of Cape Verde Shearwaters flying west before sunset was negligible, with the exception of the last 15 minutes before sunset, when numbers reached 55/15 min. (Figure 2). Numbers counted after sunrise were small (maximum 10/15 min.) and generally flew west. On one occasion, feeding behaviour of a small party of 15 birds was observed, ending in 30 minutes of rafting, after which the birds flew east. On another occasion, tens of birds associated with a group of Bottlenose Dolphins *Tursiops truncatus* passing west for a short period and then flew east.

DISCUSSION

Since counts were made by a single observer, numbers given are minimum estimates. Numbers counted at Ponta do Sol were high, with a maximum of nearly 2100 birds on the afternoon of 27 July. Given an estimated breeding population of 10,000 pairs, this implies that 10% of the world population was counted on a single evening.

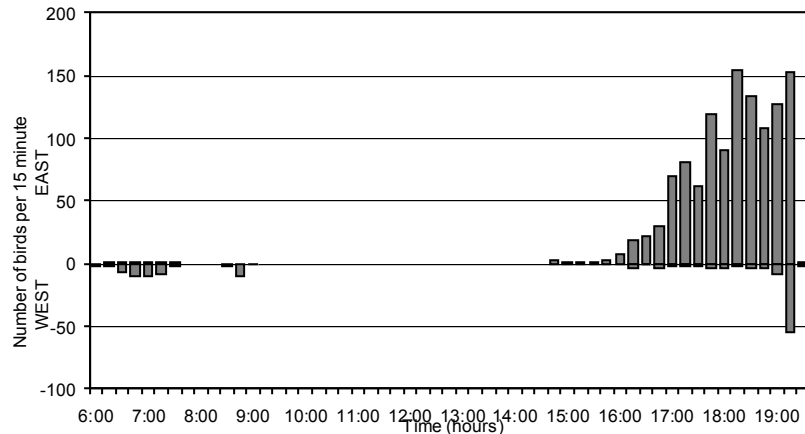


Figure 2. Mean numbers of Cape Verde Shearwaters per 15 minute period during the period 20–27 July 2005 at Ponta do Sol, Santo Antão, Cape Verde Islands. Sunrise at 6:14; sunset at 19:15; periods between 10:00 and 15:00 are given as 15 minute counts, others are completely counted.

Figuur 2. Gemiddelde aantallen Kaapverdise pijlstormvogels per kwartier, 20–27 juli 2005 op Ponta do Sol, Santo Antão, Kaapverdise Eilanden. Zonsopkomst 6:14; zons- ondergang 19:15; perioden tussen 10:00 en 15:00 zijn per kwartier geteld, andere zijn geheel geteld.

The nearest (and largest) colonies of Cape Verde Shearwater are situated on the islets of Branco and Razo, c. 75 km southeast of Ponta do Sol. Since Cape Verde Shearwaters are incubating in July, the large numbers flying east before sunset were presumably birds returning to the colonies. This resembles the behaviour of Cory's Shearwater in the East Atlantic (Azores, Madeira, Canary Islands), which arrive at the colonies after sunset (Hamer & Read 1987, Granadeiro *et al.* 1998a) and usually raft at sea while waiting for darkness.

Cory's Shearwater is known to make long (1–13 days; Granadeiro *et al.* 1998b) foraging trips to feeding grounds. Breeding Cory's Shearwaters at Selvagem Grande make foraging trips to the continental shelf of Morocco and Western Sahara, as recently established by satellite tracking (Zino *et al.* 2005). In the Azores, breeding Cory's Shearwater probably feeds close to the islands. Duration of foraging trips is probably related to the condition of the parent birds, chicks and local food availability (Babuini & Hyrenbach 2003). The feeding areas of Cape Verde Shearwater are presently unknown. To the west of Santo Antão there are a number of seamounts. These underwater mountains are known to be rich in marine life and to attract shearwaters in the southern part of the central North Atlantic (Skov *et al.* 1994). However, since observational effort in the seas around the Cape Verde Islands is lacking, no source area for

the high numbers of Cape Verde Shearwaters seen at Ponta do Sol can be given at present.

To date, there have been no published results of seawatching counts from the Cape Verde Islands. Systematic counts of seabirds from the various islands in the Cape Verde archipelago, as well as counts made from boats or planes should help to better understand behaviour and distribution of this seabird.

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Many thanks to Martin Poot for inspiring discussions and valuable literature references. Kees Hazevoet kindly provided additional information on Cape Verde Shearwaters and helped to improve the English and structure of the paper.

HOGE AANTALLEN KAAPVERDISCHE PIJLSTORM VOGELS *CALONECTRIS EDWARDSII* BIJ SANTO ANTÃO, KAAPVERDISCHE EILANDEN, IN JULI 2005

Tijdens systematische zee-rekellingen in de periode 20–27 juli 2005 op Ponta do Sol, Santo Antão, Kaapverdise Eilanden, werden 6653 Kaapverdise Pijlstormvogels *Calonectris edwardsii* geteld. De hoogste aantallen werden 2–2.5 uur voor zonsondergang gezien. De belangrijkste vliegrichting was oost. De aantallen waren 1–1.5 uur na zonsopkomst het laagst, met west als belangrijkste vliegrichting.

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DOUBLE WHITE LINES ON THE BILL OF THE
RAZORBILL *ALCA TORDA*: REMNANTS OF AN
ASSOCIATION WITH THE EXTINCT
GREAT AUK *PENGUINUS IMPENNIS*?

LAVERS J.L., MUZAFFAR¹ S.B. & JONES I.L.

Lavers J.L., Muzaffar S.B. & Jones I.L. 2006. Double white lines on the bill of the Razorbill *Alca torda*: remnants of an association with the extinct Great Auk *Pinguinus impennis*? *Atlantic Seabirds* 7(3): 127-132. *One of the diagnostic features of the Razorbill Alca torda is the distinct white line running vertically across the bill. Here we report the presence of two white bill lines in 10 wintering Razorbills from Newfoundland, Canada in addition to a small number of unreported birds from museum collections and personal records. Populations of Razorbills across their range have been divided into two major subspecies based on morphological variation, although molecular studies do not support such a subdivision. Molecular phylogeny of the auks place Razorbills as the closest relatives of the extinct Great Auk Pinguinus impennis. Multiple white bill lines were a characteristic of the Great Auk and we speculate that this variation in the bill marking in the Razorbill is an atavism, reflecting their common ancestry.*

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INTRODUCTION

Two subspecies of Razorbill are currently recognized: the larger nominate *Alca torda torda*, breeding in eastern North America, Greenland, Norway, northwestern Russia, Denmark and the Baltic; and the smaller *A.t. islandica*, breeding in Iceland, the Faeroe Islands, Britain, France, and Germany (Cramp 1985; Hipfner & Chapdelaine 2002). Breeding distributions are fairly well known, with most colonies being located on offshore islands and mainland cliffs, but there is limited information on the winter distribution of both subspecies (Hipfner & Chapdelaine 2002). The plumage of both subspecies is indistinguishable and clinal variation along a latitudinal gradient does not reveal a clear pattern (Jones 1990; Barret *et al.* 1997, Hipfner & Chapdelaine 2002).

The number of vertical grooves on the bill has previously been used to subdivide *A.t. torda* into two subspecies: *A.t. torda* and *A.t. pica* (Salomonsen 1944). However, the number of grooves in Razorbills is variable and is related to the age of the bird (Lloyd 1976; Jones 1988). The Razorbills closest relative, the extinct Great Auk *Pinguinus impennis*, had 6-12 grooves (Montevecchi &

Kirk 1996). Only one of the several grooves in Razorbills (located proximal to the base of the bill) is normally white in color. The Great Auk in comparison had all or most of its grooves white (Montevicchi & Kirk 1996). Here we report on 10 Razorbill specimens with two vertical, prominent white, bill lines collected (accidental by-catch) from various localities around Newfoundland.

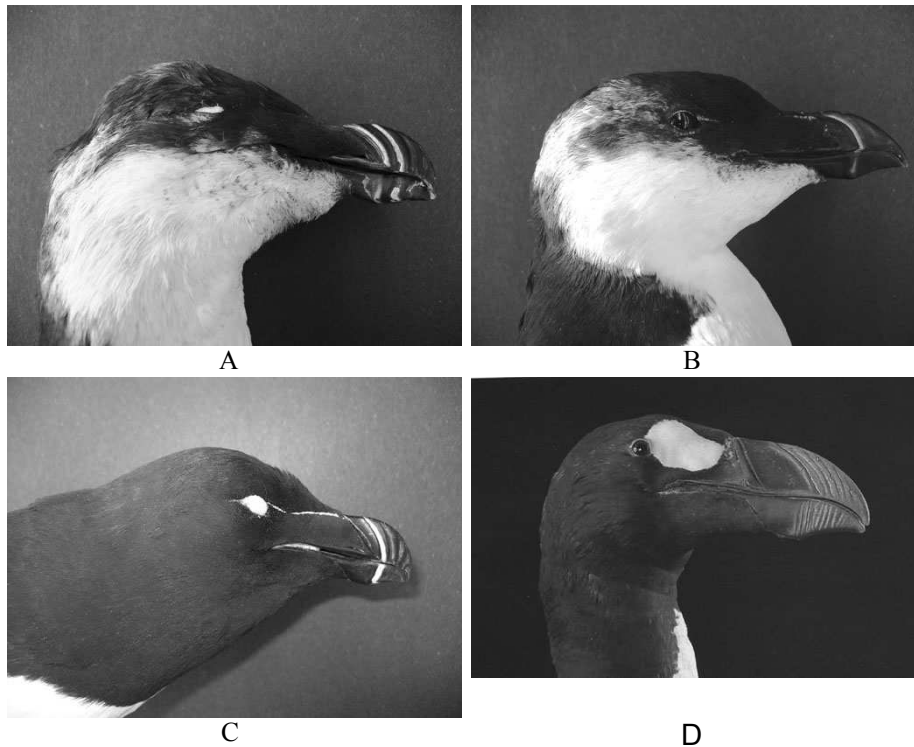


Figure 1. Adult Razorbills (a) winter plumage bird with two vertical white bill lines recovered in Newfoundland in 1997, (b) winter plumage bird with one vertical white bill line, (c) breeding plumage bird with one vertical white bill line recovered in Newfoundland in 1969, (d) extinct Great Auk (photo courtesy of E. Fuller).

Figuur 1. Adulte Alken (a) winterkleed met twee witte, verticale snavelgroeven, Newfoundland 1997, (b) winterkleed met een witte, verticale snavelgroef, (c) broedkleed met een witte, verticale snavelgroef, Newfoundland in 1969, (d) uitgestorven Reuzenalk (foto E. Fuller).

METHODS

We measured the head, bill, and wing of ten Razorbills collected in Newfoundland which exhibited two vertical, white, bill grooves and compared their measurements to those for other populations in Atlantic Canada. In addition, we contacted several museums (American Museum of Natural History, British Museum of Natural History, Cornell Museum, Provincial Museum of Newfoundland, and Tromsø University Museum) with substantial collections of Razorbills to determine if any of their specimens had this variation in bill grooves. We also contacted 13 seabird researchers from around the world to determine whether anyone else had observed or reported this double white line condition.

Table 1. Biometrics (mm) of wintering and breeding adult Razorbills in North America. Data shown as mean \pm SD (n).

Tabel 1. Biometrische gegevens (mm) van overwinterende en broedende volwassen Alken in Noord-Amerika. De gegevens zijn gemiddelden \pm SD (n).

Colony, year(s)	Plumage	Culmen Length	Bill Depth at Gonys	Bill Length	Head Bill	Wing Chord	Ref
Twillingate, Newfoundland 1997-2005	Winter	32.8 \pm 1.2 (10)	21.8 \pm 1.2 (10)	54.3 \pm 3.8 (5)	95.0 \pm 1.6 (10)	204 \pm 14.1 (10)	1
Gannet Is., Labrador 1996-2005	Breeding	33.6 \pm 1.5 (243)	23.0 \pm 0.9 (253)	53.2 \pm 2.7 (239)	94.7 \pm 2.9 (42)	204 \pm 6.0 (271)	2
Is. Ste.-Marie, Quebec 1986-1996	Breeding	32.8 \pm 1.4 (474)	23.0 \pm 1.0 (473)	Not available	Not available	208 \pm 4.9 (470)	3
Newfoundland* 2000-2004	Breeding	33.8 \pm 1.4 (23)	23.1 \pm 1.4 (23)	Not available	94.4 \pm 2.7 (23)	206 \pm 5.0 (23)	4
Machias Seal Is., New Brunswick 1995-2005	Breeding	34.7 \pm 1.6 (184)	22.7 \pm 0.9 (247)	54.3 \pm 2.0 (23)	95.0 \pm 3.1 (243)	202 \pm 5.5 (248)	5
Bay of Fundy, New Brunswick 2003	Winter	33.4 \pm 1.6 (22)	22.2 \pm 1.7 (22)	Not available	96.3 \pm 2.4 (22)	203 \pm 5.4 (22)	4

* Gull Island, Small Islands, Wadham Islands, and Musgrave Harbor (all locations are on the Avalon Peninsula) References: ¹Present study; ² I.L. Jones unpublished data; ³ Hipfner & Chapdelaine (2002); ⁴ Canadian Wildlife Service unpublished data; ⁵ A.W. Diamond, unpublished data.

RESULTS

All double white bill groove Razorbills collected in Newfoundland were in winter plumage (Figure 1a) and were collected between August and November, 1997-2005. Morphometric comparisons of these birds with other Razorbills in Atlantic Canada indicate little variation in these double line birds from other Razorbills (both in winter and breeding plumage, Table 1). Through our communications with museums, we were able to locate two additional double white bill groove specimens: one in the British Museum of Natural History (BMNH) and one in Cornell Museum. Of 100 Razorbills in the collection at BMNH, only one, a male, had the double white line condition. Of seven adult Razorbills at Cornell Museum, one bird (sex unknown) exhibited one and half white lines (instead of two full lines). A small number of Razorbills with two white bill lines were observed but never reported in Skaggerak, Norway (Tycho Anker-Nilssen and Rob Barrett, *pers. comm.*). A Razorbill banded as an adult in Iceland in 1996, recovered on the Faeroe Islands in December 2005, exhibited the double white line condition (Edward Soldaat, *pers. comm.*).

DISCUSSION

The presence of the second white bill line is seemingly inconsistent with all existing descriptions of the Razorbill (Glutz von Blotzheim & Bauer 1982; Cramp *et al.* 1985, Gaston & Jones 1998, Barrett *et al.* 2000). The frequency of this condition seems to vary by locality with approximately 1-2% of the population in Norway exhibiting double white vertical grooves (Tycho Anker-Nilssen and Rob Barrett, *pers. comm.*). However, in Newfoundland, of 29 adult Razorbills (winter and breeding plumage) examined, 10 had two vertical white grooves on their bills. The frequency of this trait in the rest of Atlantic Canada is not known as no records exist of such Razorbills in any other parts of their range. Monitoring of Razorbills further north is minimal, thus reducing the opportunity to detect double white line birds, we believe that these birds may be from further north, perhaps Greenland, and have migrated down into Newfoundland waters (all birds were collected in early fall; Lyngs 2003).

Molecular methods segregate the auks into five distinct lineages (Friesen *et al.* 1996) with Little Auks *Alle alle*, Razorbills, guillemots *Uria* spp. and the Great Auk occurring within the same lineage (Moum *et al.* 2002). Great Auks are regarded as the closest relative of Razorbills. Since Great Auks had a large number of vertical white grooves (Montevecchi & Kirk 1996, Figure 1) and no other member within that lineage has any grooves, we speculate that the presence of white grooves is an ancestral trait that emerged independently within this lineage. The Razorbills retained only one white groove, whereas the

Great Auks retained many. The observed additional white groove in the Razorbills in this study could be a case of atavism (the reappearance of an individual trait after several generations of absence), that has been documented in traits in other bird species (Raikow *et al.* 1979; Berman *et al.* 1990).

Traits observed in extant auks are a reflection of a complex evolutionary history involving changes in ecology, behavior, and biogeography (Hoberg 1992). Genetic methods have added significantly to our understanding of evolutionary relationships within the Alcidae, although major gaps still remain (Gason & Jones 1998; Moum *et al.* 2002). Further genetic studies, incorporating Razorbills from across their distribution (Moum *et al.* 2001), would shed more light on traits, such as the double white lines, and help us elucidate the phylogeny of these seabirds.

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We thank Greg Robertson for providing numerous specimens from the Canadian Wildlife Service's collection of confiscated birds. We also thank Ken Tucker for providing specimens confiscated in Lewsiporte. For their valuable input, translation of documents, and assistance in locating additional specimens, we thank Tycho Anker-Nilssen, Rob Barrett, James Butrica, Kees Camphuysen, Steve Carr, Tony Diamond, Mark Hipfner, Martin Huebeck, Steve Kress, Peter Lyngs, Jean-Francois Rail, Greg Robertson, Pierre Ryan, and Edward Soldaat. We especially thank Bill Montevecchi and Tony Gaston for their valuable comments on an earlier version of the manuscript and Errol Fuller for permission to reprint images from his wonderful book. We also thank the American Museum of Natural History, British Museum of Natural History, Cornell Museum, Provincial Museum of Newfoundland, and Tromsø University Museum for access to and information regarding their collections.

DUBBELE WITTE SNAVELGROEVEN BIJ DE ALK *ALCA TORDA*; OVERBLIJFSELEN VAN REUZENALK *PENGUINUS IMPENNIS*?

Het verticale witte lijntje over de snavel is één van de opvallendste kenmerken van de Alk *Alca torda*. In dit artikel worden tien Alken beschreven die zelfs twee witte verticale groeven hadden. De vogels waren allemaal in winterkleed en werden in Newfoundland (Canada) gevangen. Speurwerk in een aantal grote musea leverde nog enkele exemplaren op en Noorse onderzoekers wisten zich kleine aantallen te herinneren die zij nog niet eerder gerapporteerd hadden. Tegenwoordig worden bij de Alk twee ondersoorten onderscheiden. Dit onderscheid is gemaakt op grond van de gemiddelde afmetingen; moleculair werk heeft tot dusverre deze onderverdeling niet kunnen ondersteunen. De naaste verwant van de Alk is de inmiddels uitgestorven Reuzenalk *Penguinus impennis*. Deze soort had een flink aantal witte, verticale snavelgroeven en de auteurs speculeren dan ook dat de gevonden variatie in het aantal witte groeven bij de Alk een atavisme is, een terugval naar kenmerken van een gemeenschappelijke voorouder.

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EFFECTS OF SUPPLEMENTARY FEEDING ON PROVISIONING AND GROWTH RATES OF ATLANTIC PUFFIN *FRATERCULA ARCTICA* CHICKS IN NORTH NORWAY

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Dahl H.K., Barrett R.T. & Ims R.A. 2005. Effects of supplementary feeding on provisioning and growth rates of Atlantic Puffin *Fratercula arctica* chicks in North Norway. *Atlantic Seabirds* 7(3): 133-143. *After many years of a gradual change in chick diet and a supposed deterioration in feeding conditions, chicks of Atlantic Puffins Fratercula arctica were fed 50 g supplementary food per day (capelin Mallotus villosus) to test if they grew faster than control chicks, thus indicating that conditions really were suboptimal. Growth rates were, however, approximately the same as for control chicks through a near halving of provisioning rate by the experimental parents. This suggests that feeding conditions, despite a large change in diet composition, were still adequate for normal breeding.*

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INTRODUCTION

The energetic costs of reproduction in general and provisioning of young in particular are the highest an adult bird will experience throughout its lifetime, except perhaps during migration (Bryant 1997). The high energetic costs that parents incur while provisioning young are due largely to increases in foraging time, which for auks often involve very costly flight and diving activities (Bryant 1997). Life-history theory suggests that parents should regulate their reproductive investment in each breeding attempt in order to maximize their lifetime reproductive success (Stearns 1992). One would expect long-lived species such as the Atlantic Puffin *Fratercula arctica* to be restrictive in the degree to which they exhibit increased effort in one breeding attempt, because current offspring contributes relatively little to total lifetime reproduction (Ricklefs 1983, Wooller *et al.* 1992).

Some seabird parents feed chicks at a rate independent of their chicks' current requirements (Ricklefs & Schew 1994, Takahashi *et al.* 1999), suggesting that parental effort in long-lived species may be regulated to a fixed schedule in order to maximize the survival of adults (Sæther *et al.* 1993).

However, there is growing evidence for the ability of puffins to adjust provisioning in response to their chick's need (Hudson 1979, Harris 1983, Johnsen *et al.* 1994, Cook & Hamer 1997, Erikstad *et al.* 1997, Wernham & Bryant 1998), although an individual's response to its chick's need may also depend on the current body condition of the adult, the size of the chick (and hence the prospect of survival and recruitment to the population), and temporal variation in local food availability (Johnsen *et al.* 1994, Erikstad *et al.* 1997).

Evolution has favoured the adoption by puffins of a *k* life-history strategy in order to cope with high spatial and temporal variability in marine food supplies. They show delayed maturity (first breeding when 4-8 years old), lay a single egg clutch, have high adult survival rates (*c.* 96%), have a long lifetime (an average lifespan of 25 years), and have a low fecundity rate (Harris 1984, Sandvik *et al.* 2005). Because of the buffering effect of these traits against environmental changes, numbers of Atlantic Puffins would be the least influenced in the short-term. Instead, responses would probably be manifested in changes of chick diet (species composition and the amount of fish caught), chick growth rate, delayed fledging, and under extreme food shortage, chick mortality (Harris 1978, Anker-Nilssen 1987, Barrett *et al.* 1987, Barrett & Rikardsen 1992, Baille & Jones 2003).

In the early 1980s, capelin *Mallotus villosus* and sandeel *Ammodytes* spp. dominated puffin chick diet on Hornøya, NE Norway, 70° 23' N 31° 9' E (Furness & Barrett 1985). Both capelin and sandeel have high calorific, lipid and protein contents, and are thus preferred prey species for the Atlantic Puffin (Harris & Hislop 1978, Montevecchi & Piatt 1984, Furness & Barrett 1985). Food loads consisted of few large fish and both chick growth and production were considered optimal (Barrett *et al.* 1987, Barrett 2002). As a possible consequence of the large variations and overall decline in capelin stocks in the Barents Sea (Iversen *et al.* 2006), there has since been a wide diversification in the diet of Atlantic Puffin chicks on Hornøya. By 2000, the puffins were feeding their chicks on much smaller larval and juvenile fish of a variety of species and of comparatively lower energetic values than in the early 1980s (Barrett 2002). Furthermore, load mass decreased and the number of prey items per load increased, suggesting a deterioration in the diet quality (Harris 1984).

Our study addressed the feeding behaviour and growth of adult Atlantic Puffins on Hornøya following the collapse of the capelin stock between 2000 and 2003. If food availability was low, did the adults compensate in any way to ensure normal growth of their chicks? We carried out an experiment to test whether supplementary feeding had a positive effect on puffin chick growth and survival on Hornøya in 2003.

We tested the hypothesis that the fish species in the vicinity of the colony constituted a poor chick diet such that, given that the adults were foraging at a

fixed rate, chicks fed supplementary capelin grew faster than control chicks. As several studies suggest that Atlantic Puffin adults regulate their feeding effort in relation to their chick's demand (Harris 1983, Cook & Hamer 1997, Wernham & Bryant 1998), this hypothesis would be rejected if the experimental parents decreased their feeding frequency while their chicks grew at the same rate as the control chicks. That would indicate that the availability of alternative prey species was high enough to compensate for the lack of capelin, so enabling control Puffins to maintain their breeding success.

MATERIALS AND METHODS

Puffin chick growth In mid June 2003, 44 experimental burrows and 41 control burrows with an egg or young chick were fitted with inspection lids and marked with a numbered stake. The control and experimental nests were all chosen in the same area with approximately the same burrow density, slope and distance to the cliff edge, as these parameters may each affect breeding success (Rodway *et al.* 1998). Where a chick was already present it was aged by comparing wing and culmen length with those of known-age control chicks.

The study was conducted from 15 June-5 August 2003. After the first chick had hatched, all nests were inspected every three days and all chicks were weighed to the nearest 5 g and their wing length (maximum flattened chord, including down but minus the little tuft at the end) was measured to the nearest 1 mm using a stopped ruler. The culmen was measured to the nearest 0.1 mm using vernier callipers. As the study ended before the chicks were fully grown, growth rates were compared statistically until 34 d post-hatching.

Supplementary feeding of experimental chicks Chicks were fed with recently thawed capelin. Each daily ration was cut in *c.* 3.0×0.7 cm slices, weighed on an electrical balance, and placed in small plastic bags. From the fourth to the seventh day after hatching each chick received 30 g (\pm 0.1 g) per day of thawed capelin, which was placed in the nest chamber. Thereafter they were given 50 g (\pm 0.1 g) per day, thereby approximately following the protocols of Harris (1983) and Cook & Hamer (1997). All the fish appeared to be eaten in addition to those which the adults brought, and the adults were presumed not to eat the food supplement because they do not take fish from the floor in captivity (Wernham & Bryant 1998).

Food choice Food items being brought into the colony were identified, counted and their lengths estimated (in relation to bill size) using Zeiss 10×40 binoculars. This method was used rather than catching fish-carrying adults in

mist nets in order to reduce the loss of very small food items in the vegetation, and also to reduce disturbance in the colony.

However, 26 food samples were also collected by catching fish-carrying puffins with a noose pole or at burrow entrances. They were used as controls for the visual identification and estimates of numbers and sizes of prey items. The mass of each observed food item was integrated from its estimated length based on the length/mass relationships determined from samples of the same species collected in the field from adult puffins in the same season (RTB unpubl. data). The energy content (kJ g^{-1} wet weight) of each food item was calculated using published values of fish caught in summer since prey species often have variable energy content throughout the year (Montevicchi and Piatt 1984).

Feeding frequency Comparative rates at which control and experimental chicks were fed were determined during 2-4 hour watches of 5-14 experimental burrows for a total of 39 hours. In a neighbouring area, 11-13 control burrows were simultaneously watched from another hide by another investigator, thus allowing direct comparisons to be made without having to consider variations due to weather or time of day (Harris & Hislop 1978). The observations were made from 14 June-3 August at randomly chosen hours from 0900 to 2320 hrs. A feed was recorded every time an adult with fish entered the burrow. Feeding frequency observations began at least three days after the first supplementary feeding in order to allow the adults to adjust to the experimental conditions (Hudson 1979, Harris 1983, Wernham & Bryant 1998).

The average number of feeds per hour was calculated for each chick during each watch, and each chick was assigned to a 3 day age class.

Statistical methods Analyses of growth patterns (weight, wing and culmen length) were carried out using mixed effects linear models with age, treatment group (control vs experiment) and the interaction age*treatment group as fixed effects and chick identity as a random effect nested in the treatment effect. Temporal autocorrelation between sequential measurements of the same chick was modelled as a first order process (AR-1 process). As the field season ended before the chicks were fully grown, there were few observations of the size variables for chicks older than 34 days. Any such observations were excluded from the analyses in order to achieve convergence of the numerical algorithm (restricted maximum likelihood). Logarithmic transformations (\ln) were necessary for growth variables to obtain stable variance of the residuals. All mixed model analyses were executed in PROC MIXED SAS version 6.1.

As the feeding frequency data were skewed with respect to chick age, it was not possible to take age into account using a similar analysis as that for growth pattern. Thus, a simple ANOVA model with mean feeding frequency

(number of feeds per hour) at each nest over the whole observation period was applied. No transformation was necessary for this analysis.

RESULTS

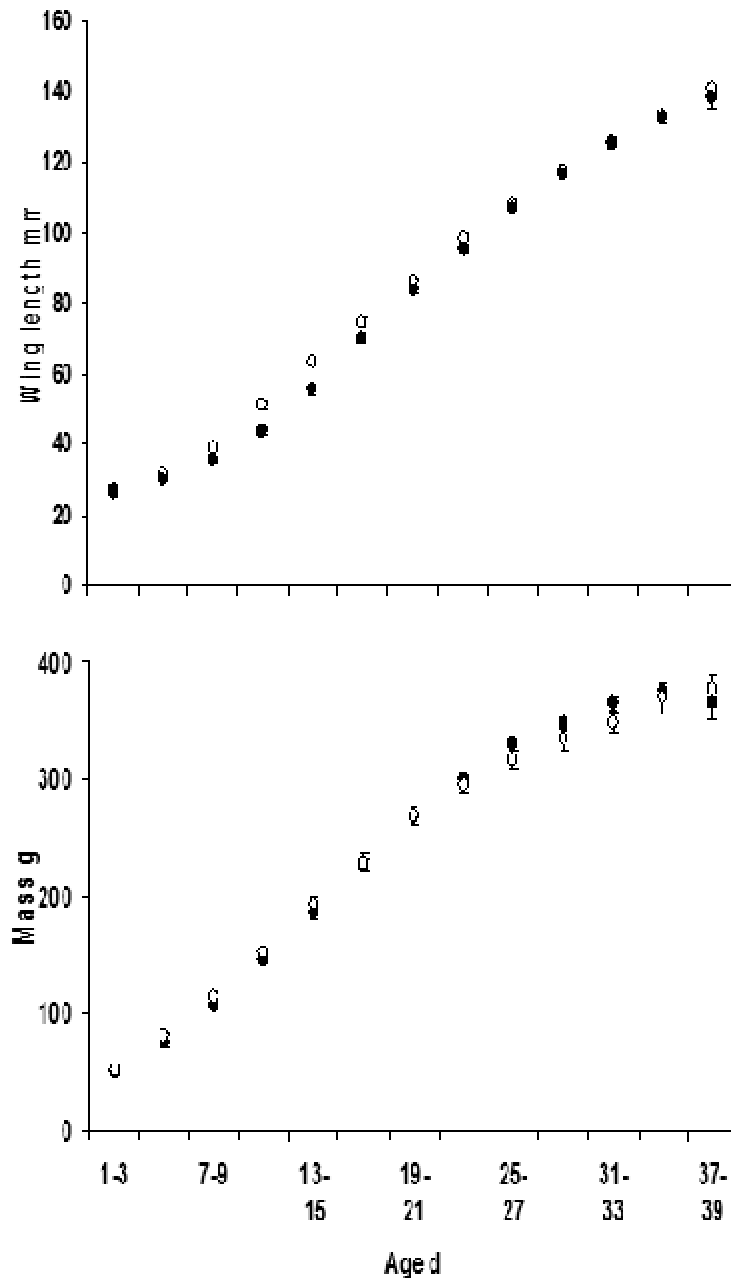
Puffin chick growth Although the growth curves were very similar (Fig. 1), there was a significant interaction between treatment and age in both wing length and body mass at least until day 34 (see Methods). The interaction on body mass ($F_{11,648} = 2.24$, $P = 0.011$) was mainly due to a tendency of experimental chicks to become relatively heavier at older age, whereas a stronger interactive effect on wing length ($F_{11,648} = 12.73$, $P < 0.001$) was due to longer wings in young control chicks. Also, the main effect treatment was significant for wing length ($F_{1,77} = 7.66$, $P < 0.007$), whereas it was not for body mass ($F_{1,77} = 0.000$, $P < 0.99$). Although the experimental chicks tended to be heavier at ages > 25 d, none of the differences in mean mass for each age class was significant (t-tests, $P > 0.05$).

Feeding frequency There was a large overall difference in feeding frequency between experimental and control chicks ($F_{1,27} = 10.87$, $P = 0.003$). The estimated overall feeding frequency in the experimental group (0.25 times per hour, 0.16-0.33 95% CI) was 60% the rate of the feeding frequency of the control group (0.42 times per hour, 0.35-0.53 95% CI). A plot of feeding frequency in the different age groups did not suggest any consistent differences among age groups in experimental or control chicks (Fig. 2).

The chicks' daily food intake The overall mean number of fish per load brought to the control chicks was 8.2 (± 0.28 SE), whereas the mean load mass (and energy equivalent) of fish was 8.1-8.8 g (48-55 kJ) for 12-15 and 20-25 day old chicks respectively. The control chicks were fed 9-10 times per day and so received 70-90 g or approximately 450-550 kJ d⁻¹. The experimental chicks were fed at 60% of the rate of control chicks and, assuming no differences in bill load size (as documented by Cook & Hamer 1997, Gjerdrum 2004), thus received 40-50 g (270-330 kJ) from their parents. With a supplementary ration of 50 g capelin per day (mean length 166.5 mm \pm 1.3 SE, $n = 50$, energetic equivalent = 5.6 kJ g⁻¹, Furness & Barrett 1985), the experimental chicks therefore ate an equivalent of 550-610 kJ d⁻¹.

DISCUSSION

Chick diet and feeding frequency In 2003, the diet of the Puffin chicks was varied and consisted of gadoid fish, sandeels, herring, capelin, and unidentified



Opposite page: figure 1. Growth rate (wing length and body mass) of experimental (dots) and control (circles) Atlantic Puffin chicks on Hornøya, 2003. Means \pm 1 SE. N = 25-36 except two oldest age classes where N = 7-23.

Tegenoverliggende pagina: figuur 1. Groeisnelheid (vleugellengte en lichaamsgewicht) van bijgevoerde (punten) en 'controle-kuikens' (cirkels) van Papegaaiduiker op Hornøya, 2003. Gemiddelden \pm 1 SD. N = 25-36 behalve de twee oudste leeftijdsklassen, waarbij N = 7-23.

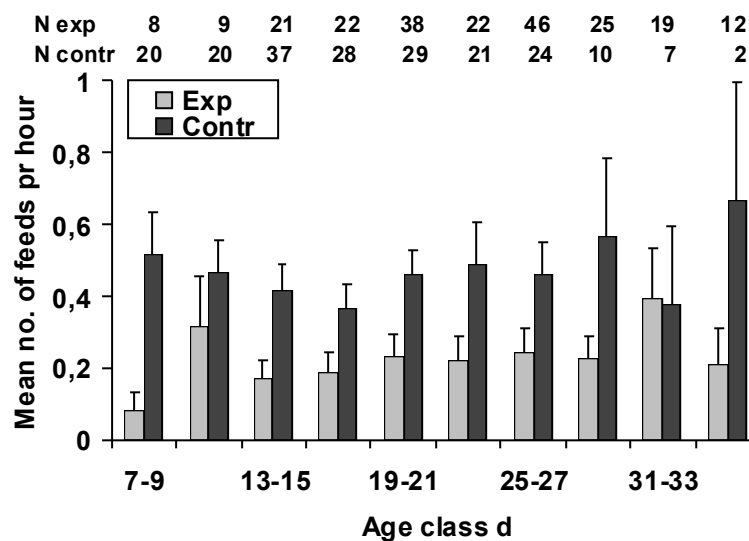


Figure 2. Feeding frequency (no. of feeds $h^{-1} \pm 1$ SE) with respect to age of experimental and control Atlantic Puffin chicks on Hornøya, 2003. N is number of chicks in each age class.

Figuur 2. Voederfrequentie (voerbeurten $h^{-1} \pm 1$ SD) in relatie tot de leeftijd van bijgevoerde en 'controle-kuikens' van Papegaaiduikers op Hornøya, 2003. N is het aantal kuikens in iedere leeftijdsklasse.

juvenile fish. Small, 0-group gadids (cod and saithe *Pollachius virens*) dominated in number, whereas small sandeels (mean length 87 mm) dominated in mass (RTB unpubl. data). The overall mean number of fish per load brought to chicks was relatively high (8.2 ± 0.28 SE), and the mean load mass (and energy equivalent) of fish was 8.1-8.8 g (48-55 kJ). A comparison with data from years dating back to 1981 showed a considerable change in diet from one dominated by large capelin and sandeels to one composed of many small larval and juvenile fish. Mean numbers of fish per load increased from 2-3 in the early

1980s to 8-10 in 2003, while the mean load mass dropped from 11-12 g to 8 g, both suggesting a gradual deterioration in the availability of high quality fish (Barrett 2002, this study).

Parental food provisioning is a readily adjustable component of reproductive effort in long-lived seabird species, and many studies have demonstrated an ability to regulate reproductive effort through adjustments of provisioning rates in response to the chick's need (e.g. Johnsen *et al.* 1994, Bolton 1995, Hamer *et al.* 1998, Granadeiro *et al.* 2000, Jodice *et al.* 2002). While the degree to which parents adjust provisioning may be influenced by species-specific constraints such as the assimilation capacity of the digestive tract (Ricklefs 1992), body condition of the adults (Johnsen *et al.* 1994) or nocturnal, single-meal provisioning habits (Takahashi *et al.* 1999), any increase probably reaches a threshold above which further investment by the parents compromises future survival (Erikstad *et al.* 1998).

The supplementary feeding on Hornøya resulted in a significant decrease in the experimental parents' feeding frequency demonstrating that adult Puffins can reduce food provisioning in response to a decrease in their chick's nutritional requirements. This corroborates other studies where conditions have been experimentally improved for e.g. the Atlantic Puffin (Johnsen *et al.* 1994, Cook & Hamer 1997, Wernham & Bryant 1998), the Horned Puffin *F. cirrhata* (Harding *et al.* 2002), and the Tufted Puffin *F. corniculata* (Gjerdrum 2004).

Chick growth Several studies have suggested that mass increase is a more sensitive measurement than the somatic growth of e.g. bill or wing length (Ricklefs & White 1975, Gaston 1985). An experimental study by Øyan and Anker-Nilssen (1996) indicated that growth of the skull is given highest priority in food-stressed puffin chicks, followed by the culmen, forearm, middle toe, tarsus, 2nd primary and, lastly, mass increase.

Despite supplementary feeding, however, there were no significant differences in mass increase during the period of maximum growth between experimental and control chicks in this study, suggesting that both sets of chicks grew near their physiological maximum rate. Harris (1978) showed that supplementary feeding of puffin chicks had a greater effect on the chick's mass at one Scottish colony, St Kilda, where feeding conditions were poor, than it had at another, the Isle of May, where feeding conditions were favourable. This suggests that puffin chick growth is limited by the maximum rate at which adults can supply food when feeding conditions are poor. The non-significant difference in mass growth rate between experimental chicks and control chicks in this study suggests that, despite a considerable change over time towards a supposedly poorer diet (Barrett 2002), the feeding conditions were still adequate for the chicks. It seems that, despite the reduction in size and increase in number

of fish fed to the chicks, the amount and quality were nevertheless high enough to maintain normal chick growth. However, the implications of any possible increase in effort required by the parents to catch a larger number of fish, such as a possible reduction in adult body condition at the end of the breeding season, remain to be investigated.

Furthermore, because change in mass is a more sensitive parameter than change in wing length (Ricklefs & White 1975, Gaston 1985, Øyan & Anker-Nilssen 1996), it is unlikely that the wings were actually longer in the young control chicks than in experimental chicks as the results suggest. The differences are most likely to be due to inconsistencies in the measurements, which were made by two different persons. That there were differences in measurements of young chicks only was probably due to the difficulty of accurately measuring downy wings, whereas the measuring method readily became standardized when the feathers erupted. The fact that supplementary-fed chicks tended to be heavier than controls towards the end of the experiment (Fig. 1; also shown by Hudson 1979, Cook & Hamer 1997, Wernham & Bryant 1998), however, suggests that experimental chicks were willing to eat more food than their parents would normally have provided at the end of the season, which in turn may accord some post-fledging survival advantages (Hamer *et al.* 1991).

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EFFECT VAN BIJVOEDERING OP VOEDEREN EN GROEISNELHEID VAN KUIKENS VAN PAPEGAAIDUIKER *FRATERCULA ARCTICA* IN NOORD-NOORWEGEN

Na vele jaren van een geleidelijke verandering in het dieet van kuikens van Papegaaiduikers *Fratercula arctica* en een veronderstelde achteruitgang in foerageeromstandigheden, werden kuikens bijgevoerd met 50 g lodde *Mallotus villosus* per dag om te controleren of ze sneller groeiden dan de 'controle-kuikens'. Daarmee zou aangetoond kunnen worden dat de omstandigheden inderdaad suboptimaal zijn. De groeisnelheid van de bijgevoerde kuikens was echter ongeveer hetzelfde als voor 'controle-kuikens' als gevolg van een afname van de voederen door de ouders. De resultaten suggereren dat foerageeromstandigheden, ondanks een grote verandering in de samenstelling van het dieet, nog steeds voldoende zijn om normaal te broeden.

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