

Diving Patterns in the Antarctic Shag

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Abstract.—The diving patterns of the Antarctic Shag (*Phalacrocorax bransfieldensis*) were studied by direct observation on individuals foraging at Harmony Cove, Nelson Island, South Shetland Islands, during the 1995/96 and 1996/97 breeding seasons. The individuals observed foraged in shallow waters, mainly solitarily and presumably dived aerobically. The shags displayed relatively short diving bouts composed of few dives. During the 1995/96 breeding season, the duration of the dives decreased with the increase in the number of dives per bout and increased with the diving depth. These relationships were not statistically significant in 1996/97. In both seasons, the duration of the dives was positively related with both the surface resting time preceding and succeeding the dive, which may indicate that these birds display anticipatory or reactive dives probably according to the foraging conditions. Shags at the surface were seen swallowing fish longer than 15 cm; smaller fish as well as invertebrates may have been ingested underwater. The mean diving efficiencies of the bouts fall within the range reported for phalacrocoracids, but values of diving efficiency below unity were observed. Received 14 October 2003, accepted 3 June 2004.

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The Antarctic Shag (*Phalacrocorax bransfieldensis*) (formerly known as the Blue-eyed Shag *Phalacrocorax atriceps bransfieldensis*) breeds along the Antarctic Peninsula and the South Shetland Islands (Orta 1992) during the austral summer and feeds close inshore mainly on demersal-benthic fish (Casaux and Barrera-Oro 1993; Casaux *et al.* 2002). Among fish, the Bullhead Notothen (*Notothenia coriiceps*) followed by the Antarctic Spiny Plunderfish (*Harpagifer antarcticus*) and the Gaudy Notothen (*Lepidonotothen nudifrons*) at the South Shetland Islands (Casaux *et al.* 1998) and the Bullhead Notothen and the Humphead Notothen (*Gobionotothen gibberifrons*) at the Antarctic Peninsula (Casaux *et al.* 2002) are their main prey.

Other aspects of the foraging behavior of this species have been studied. Favero *et al.* (1998) and Casaux *et al.* (2001) reported that male Antarctic Shags prey more intensively on larger fish than females. The sexual differences in the composition of the diet (Casaux *et al.* 2001) may be explained by the fact that males are heavier and larger than females (Casaux and Baroni 2000), that individuals presents sexual differences in daily foraging patterns (Bernstein and Maxson

1984; Casaux 1998; Favero *et al.* 1998), that individuals of both sexes partitioned the use of the foraging depths with females diving deeper (Casaux *et al.* 2001), and that males deliver more food to the chicks and visit the nest more often than females (Casaux 1998; Favero *et al.* 1998). Despite these studies, there is no information available on the diving strategy of this species except for few dive and inter-dive time measurements (Kooyman 1975; Bernstein and Maxson 1985).

The foraging behavior of seabirds at sea and their population dynamics may be sensitive to changes in food availability (Cairns 1987; Burger and Piatt 1990; Montevecchi 1993). During the last decade, the number of shags breeding in colonies at the South Shetland Islands has decreased (Casaux and Barrera-Oro unpublished) in parallel with changes observed in the structure of the coastal inshore fish fauna (see Barrera-Oro and Marschoff 1991; Barrera-Oro *et al.* 2000). Within this context, more studies on the foraging behavior and breeding biology of this shag are required to understand the factors regulating their populations and the possible responses to such factors. Thus, the aim of this study is provide new information

on the foraging behavior of the Antarctic Shag, focusing on a topic scarcely investigated such as the diving patterns.

MATERIAL AND METHODS

The information in this study was obtained from adult Antarctic Shags diving at Harmony Cove ($62^{\circ}18'S$, $59^{\circ}12'W$; 4.5 km^2 ; 40 m maximum depth), Nelson Island, South Shetland Islands, from 22 November 1995 to 10 February 1996 (hereafter 1995 breeding season) and from 17 November 1996 to 6 January 1997 (hereafter 1996) (Fig. 1). Based on banded individuals (males on the right leg and females on the left leg) Casaux *et al.* (2001) reported that 97% of the individuals observed during the 1996 breeding season in inter-diving bout resting periods on the western coast of Harmony Cove were males. Thus, it is possible that the observations reported in this study also were mostly from males but the sex of birds studied was not known.

Observations were made from the western coast of the cove in Harmony Point. To prevent errors in the identification of individuals, observations were only performed on shags foraging solitarily, which was the feeding strategy most frequently used. For analysis, the diving activity was organized into diving bouts (sequence of dives and inter-dive surface resting periods performed by the shags from arrival at the sea to the return to the colony or to the roost). Only complete diving bouts were considered and their duration (as defined above) were recorded, as well as the duration and number of dives per bout, the duration of the inter-dive surface resting periods, the duration of the inter-bout resting periods, the minimum number of "successful dives" per bout (defined as the post-dive surface periods where the shags were seen swallowing prey), and the diving depths (estimated from the nautical chart of the Servicio de Hidrografía Naval Argentino No. 711 and from my own depth measurements at specific points of the cove). Given that the main prey of the Antarctic Shag at the South Shetland Islands are demersal-benthic fish (see Casaux *et al.* 1998, for review) which display limited vertical movements (Casaux *et al.* 1990), it is assumed that this bird at the study area forage on the bottom (Casaux and Barrera-Oro 1993). Thus, sea depth at the foraging site was considered as the diving depth. The maximum diving depth recorded in this

study (30 m) coincided with the maximum depth within the area of Harmony Cove under observation; Casaux *et al.* (2001) reported that during the study period out of Harmony Cove these shags dived to 112.6 m. Timing was recorded to the nearest second.

The diving efficiency was measured as the ratio of diving time to surface time (Dewar 1924). For this estimation the last dive of the bout was not considered, because before flying, the individuals invested some time in bathing or preening so that the succeeding surface time did not reflect the recovery after the dive. Given that the ascent and descent velocities were not measured, the foraging efficiency was not estimated.

The taxonomy and nomenclature of the Blue-eyed Shag group, which include the Antarctic Shag, is complex and still subject to considerable discussion and revision. In this study I adopt the nomenclature given in Orta (1992).

RESULTS

The characteristics of the complete bouts observed during the 1995 and 1996 breeding seasons, as well as the statistical results of the comparisons between seasons, are presented in Table 1.

The duration of the bouts increased with the number of dives per bout in 1995 ($r^2_{23} = 0.56$, $P < 0.001$, $y(\text{sec}) = 264.5 + 32.23 \cdot x$) but not in 1996 ($r^2_{15} = 0.21$, n.s.) (Fig. 2). The duration of the bouts was not significantly related with the mean diving depth of the bout in both seasons ($r^2_{23} = 0.04$, n.s., and $r^2_{15} = 0.17$, n.s., respectively).

The mean number of dives per bout was not significantly related with the mean diving depth of the bout ($r^2_{23} = 0.02$, n.s., for 1995, and $r^2_{15} = 0.06$, n.s., for 1996). In 1995, the mean duration of the dives within bouts increased with the mean diving depth of the bout ($r^2_{23} = 0.50$, $P < 0.001$, $y(\text{sec}) = 32.74 + 1.87 \cdot x(\text{m})$) (Fig. 3) but decreased with the number of dives per bout ($r^2_{23} = 0.19$, $P < 0.05$, $y(\text{sec}) = 48.32 - 0.98 \cdot x$); these relationships were not statistically significant in 1996 ($r^2_{15} = 0.16$, n.s., and $r^2_{15} = 0.16$, n.s., respectively).

The mean diving efficiency of the bouts observed in both seasons was not significantly related with the mean duration of the dives ($r^2_{19} = 0.04$, n.s., for 1995; $r^2_{12} = 0.05$, n.s., for 1996), with the number of dives per bout ($r^2_{19} = 0.02$, n.s., and $r^2_{12} = 0.02$, n.s.), nor with the mean diving depth ($r^2_{19} = 0.02$, n.s., and $r^2_{12} = 0.01$, n.s.). The duration of the dives was positively related both with the rest-

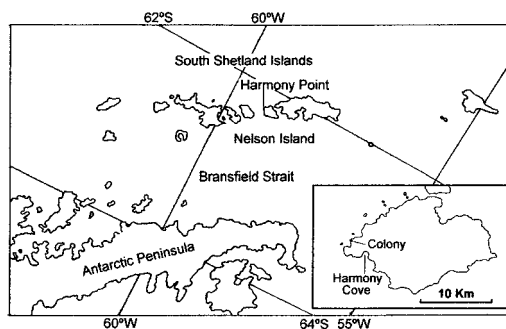


Figure 1. Map showing the location of Harmony Cove at Nelson Island, South Shetland Islands.

Table 1. Number of diving bouts and dives observed in the Antarctic Shag (*Phalacrocorax bransfieldensis*) at Harmony Cove, South Shetland Islands, during the 1995 and 1996 breeding seasons and comparison between seasons of the duration of diving bouts and dives, number of dives per bout, diving depth and efficiency within bouts, and duration of the inter-bout resting period. Values are expressed as mean \pm 1 standard deviation.

	1995	1996
No. of bouts observed	25	17
No. of dives observed	225	88
Duration of the bouts (sec) (n.s.)	552 \pm 336; N = 25	521 \pm 321; N = 17
No. of dives per bout (*)	9.0 \pm 7.9; N = 25	5.2 \pm 8.2; N = 17
Diving depth (m) (n.s.)	6.7 \pm 8.5; N = 25	9.2 \pm 10.0; N = 17
Inter-bout resting period (sec) (n.s.)	1923 \pm 2186; N = 6	2236 \pm 1734; N = 8
Duration of the dives (sec) (**)	39.6 \pm 17.9; N = 25	67.4 \pm 37.4; N = 17
Diving efficiency (n.s.)	2.6 \pm 2.2; N = 21	4.3 \pm 7.8; N = 14

Mann-Whitney U-test, n.s.: non significant; *P < 0.05; **P < 0.01.

ing surface time preceding ($r^2_{190} = 0.20$, $P < 0.001$, $y(\text{sec}) = 1.70 + 0.45 \cdot x(\text{sec})$, in 1995, and $r^2_{71} = 0.48$, $P < 0.001$, $y(\text{sec}) = 1.65 + 0.76 \cdot x(\text{sec})$, in 1996) and succeeding ($r^2_{190} = 0.19$, $P < 0.001$, $y(\text{sec}) = 2.10 + 0.44 \cdot x(\text{sec})$, in 1995, and $r^2_{71} = 0.36$, $P < 0.001$, $y(\text{sec}) = 3.66 + 0.62 \cdot x(\text{sec})$, in 1996) the dive. The efficiencies of the dives preceding those when a prey was swallowed on the surface (mean 6.10, SD \pm 8.87) were significantly higher (Mann-Whitney U-test, $z = 3.65$, df 26, $P <$

0.001) than those when the prey was ingested (mean 1.15, SD 0.76).

In only 44% and 35% ($\chi^2_1 = 1.69$, n.s.) of the bouts observed in 1995 and 1996 respectively (Table 1) (or 12% and 4% of the dives observed respectively; $\chi^2_1 = 8.86$, $P < 0.01$) the shags were observed swallowing a fish at the surface. This does not necessarily imply that the remaining bouts or dives were unsuccessful. Fish were manipulated in order to be swallowed head-first. All these fish were

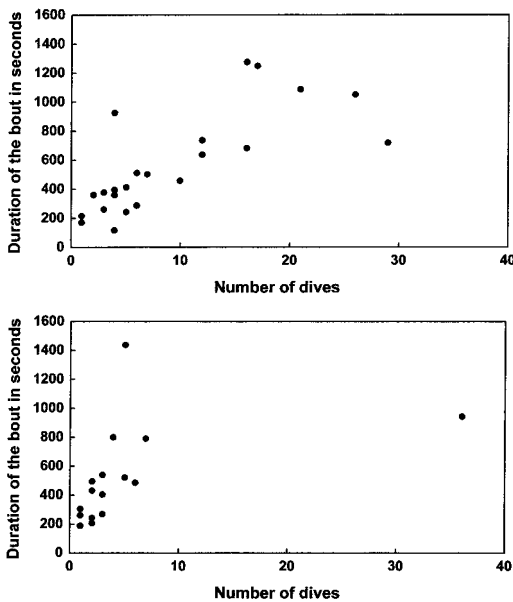


Figure 2. Relationship between the duration of the bouts and the number of dives per bout observed in the Antarctic shag at Harmony Cove during the 1995 (upper) and 1996 (lower) breeding seasons.

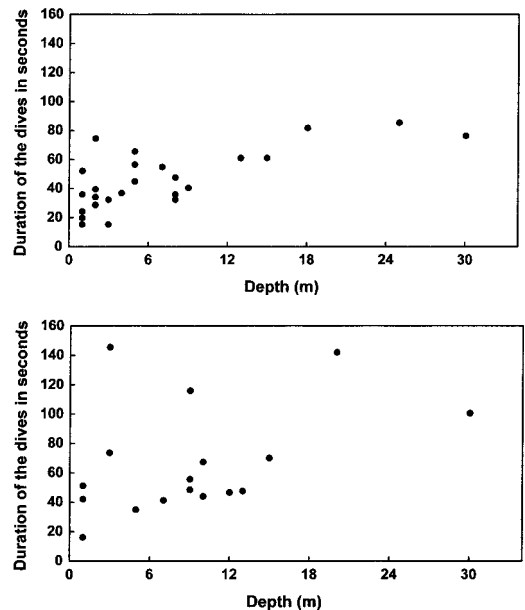


Figure 3. Relationship between the mean duration of the dives within the bouts and the mean diving depth within the bouts performed by the Antarctic Shag at Harmony Cove during the 1995 (upper) and 1996 (lower) breeding seasons.

tentatively identified as Bullhead Notothen and their size range (estimated by comparison with the size of the shags) was 15-30 cm. In 18 (72%; the two occasions when the fish were kleptoparasitized by Kelp Gulls (*Larus dominicanus*) were not considered, see below) and 4 (67%) of the "successful bouts" recorded in 1995 and 1996 respectively, the shags ended the diving bout immediately after swallowing the first fish brought to the surface. In the remaining cases, the shags continued diving and were seen swallowing up to three fish at the surface.

DISCUSSION

The Antarctic Shag at the Antarctic Peninsula frequently forage in groups of up to 200 individuals (Bernstein and Maxson 1985), but at Harmony Cove this shag usually foraged solitarily but occasionally in groups of up to eight individuals. Foraging in groups is advantageous when shags forage in the water column or in turbid waters (Van Eerden and Voslamber 1995) or when the prey is patchy distributed (Orians and Pearson 1979). The main prey of the Antarctic Shag in the study area, the Bullhead Notothen (Casaux *et al.* 1998), is a demersal-benthic fish with a strong site fidelity (Barrera-Oro and Casaux 1996) and uniformly distributed on rocky bottoms with algal beds, which may explain why solitary foraging is the most common strategy at Harmony Cove, an area with clear waters.

The dive times recorded in this study are similar or slightly shorter than those reported by Kooyman (1975) and Bernstein and Maxson (1985) for individuals of this species at the Antarctic Peninsula. The absence of information on diving depths or diving/inter-diving time rates in those studies prevent further comparisons.

The lower number of dives per bout observed in 1996 suggest that foraging conditions were better than in 1995. However, this could be an artefact since most of the bouts initiated close to the coast in 1996 were interrupted, perhaps due to a scarcity of prey in very shallow waters, and the shags moved to deeper (and not observable) waters. Com-

plete bouts recorded in 1996 were therefore only the more successful ones. The duration of the dives, the proportion of "successful dives" and the interruption of the bouts suggest more difficult foraging conditions in 1996 compared to 1995. This is supported by the fact that shags in 1996 spent more time foraging per day, suffered a higher chick mortality rate, and emancipated chicks lighter in weight (R. Casaux and A. Baroni, unpubl.). Although speculative and without considering the dives outside Harmony Cove, these concurrent observations suggest that changes in fish abundance/distribution with depth might influence the foraging behavior and performance of the Antarctic Shag, and the reproductive output (see also Debout *et al.* 1995).

Croxall *et al.* (1991) considered for the South Georgia Shag (*P. georgianus*) at South Georgia three diving categories: "deep dives" (at depths of 35-116 m), "shallow dives" (to 21 m) and "intermediate dives" (21-35 m). According to these categories 84% of the dives observed at Harmony Cove were "shallow dives". Since the limit for aerobic dives estimated for the South Georgia Shags is 174 seconds (Wanless *et al.* 1992), all the dives observed at Harmony Cove may have been aerobic (maximum dive duration: 171 sec). However, an aerobic dive is not only determined by the time spent submerged, but also by the oxygen reserves at the beginning of the dive, for which I have no data.

Except when the physiological limits or the time available to forage are exceeded, it is expected that the diving bouts finish once the foraging expectation is achieved. However, shags were seen swallowing a prey on the water surface in only 44% and 35% of the diving bouts recorded in the 1995 and 1996 breeding seasons respectively. Given that the diving times were far from the aerobic limit and that the duration of the bouts were markedly shorter than those observed in shags with similar diving abilities (see Croxall *et al.* 1991), it is logical to expect that some of the prey were ingested under water. All the fish ingested on the water surface were tentatively identified as Bullhead Notothen longer than 15 cm. Those identifications were

partially confirmed when two *N. coriiceps* specimens caught by shags were kleptoparasitized by Kelp Gulls and recovered from their nests in 1995. Fish smaller than 15 cm and invertebrates were frequently found in the diet of these shags during the studied period (Casaux *et al.* 2001). It is probable that prey longer than 15 cm in length are difficult for shags to swallow under water and must be eaten at the surface; smaller prey could be ingested during the dive (see also Croxall *et al.* 1991). Thus, direct observation is not an accurate method to estimate foraging success and number/type of prey ingested per dive in the Antarctic Shag. This prevents speculation on how the time within the bout is administered in relation to the prey catch rate.

The mean diving efficiency within bouts observed in both seasons fall within the range reported by Cooper (1986) for phalarocoracids. However, the lowest diving efficiency observed at Harmony Cove was 0.2, a value largely lower than those reported by Cooper (1986) for the family (see also Croxall *et al.* 1991; Kato *et al.* 1992). This finding invalidates the hypothesis of Ridoux (1994), suggesting that efficiencies close to unity indicate the dive duration limit of shags.

During the chick rearing period the Antarctic Shag at Harmony Cove frequently caught more than one prey per bout (see also Casaux *et al.* 2001). Thus, some of the surface periods registered here could be influenced by prey handling and swallowing time (see Lea *et al.* 1996) which affect the estimation of the diving efficiency. At Harmony Cove, the efficiencies of the dives (*sensu* Dewar 1924) immediately preceding those when a prey was swallowed on the surface were significantly higher than those when the prey was ingested supports this hypothesis. Therefore, for the interpretation of parameters which consider the inter-diving times (such as diving efficiency, foraging efficiency, etc.) the activity of the individuals on the surface should be carefully considered.

Lea *et al.* (1996) described three diving strategies: 1) reactive breathing, when the individuals stay on the surface as long as is needed to replenish oxygen stores to a fixed level; 2) anticipatory breathing, if individuals

anticipate the length of their next dive loading themselves with oxygen accordingly and then stay under water until their oxygen stores is reduced to a fixed level; and 3) when individuals operate well within their oxygen capacity on individual dives and do not replenish oxygen to a fixed level between dives. At Harmony Cove, the diving times were positively related both with the surface resting time preceding and succeeding the dive. Given that the Antarctic Shag prey mainly on demersal-benthic fish sheltered in rocky bottoms with algal beds, it is expected that this bird cannot predict accurately the time required to encounter prey, therefore the reactive dive seems to be the most appropriated strategy. However, it was frequently observed that shags emerged and submerged after a very brief period on the surface to emerge again with a large fish. This may indicate that when a prey is detected but there is not enough oxygen reserves to swallow it at the bottom or to carry it to the surface, the shags replenish the reserves up to a minimum level required to do it, thus probably performing an anticipatory dive. Evidence indicating that birds modify the diving strategy according to prey availability was provided by Ydenberg and Forbes (1988) and Ydenberg and Clark (1989). In this sense the diving strategy seems to be an indicator of the foraging conditions rather than being a feature of the species.

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