

FORAGING PATTERNS OF THE ANTARCTIC SHAG *PHALACROCORAX BRANSFIELDENSIS* AT HARMONY POINT, ANTARCTICA

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ABSTRACT

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During the 1995 and 1996 summer seasons, the foraging patterns of the Antarctic Shag *Phalacrocorax bransfieldensis* were studied by direct observation at Harmony Point, Nelson Island, South Shetland Islands. During pre-laying and incubation, individuals of both sexes usually foraged once a day—females early in the morning and males when their partners returned to their nests. Due to increasing energy requirements at the nest, rearing individuals increased the daily time invested in foraging activities, displaying more—but shorter—foraging trips. The reduction in the duration of the foraging trips through the breeding season suggests that Antarctic shags budget their activities to buffer variable food abundance or energy requirements at their nests. Here, we discuss the possibility of using the foraging parameters measured in this study in ecosystem monitoring programs.

Keywords: Cormorants, feeding effort, South Shetland Islands, ecosystem monitoring

INTRODUCTION

The Antarctic Shag *Phalacrocorax bransfieldensis* inhabits the Antarctic Peninsula and the South Shetland Islands (SSI). The estimated population size is 10900 breeding pairs (Orta 1992). Although this figure might be an underestimate, a steady decline in the number of breeding pairs has been reported over the last 25 years at several colonies within their breeding range (Woehler *et al.* 2001, Naveen *et al.* 2000, Casaux & Barrera-Oro 2006). The most likely explanation for the decrease at the SSI is the continuing low availability of formerly abundant fish prey, *Gobionotothen gibberifrons* and *Notothenia rossii*, in inshore waters due to commercial fishing at the end of the 1970s (Casaux *et al.* 2002, Casaux & Barrera-Oro 2006, Ainley & Blight 2009).

Regarding foraging strategies, several studies have documented daytime activity rhythms in colonial seabirds (Snow 1963, Muller-

Schwarze 1968, Burger 1976). Curiously, for the Antarctic Shag at the Antarctic Peninsula, Bernstein & Maxson (1984) reported synchronised, colony-wide, daily foraging rhythms for each sex. Later, these activity patterns, as well as changes throughout the breeding season, were also reported for Antarctic Shags at the SSI (Favero *et al.* 1998). However, the effect of brood size and chick growth on adult activity patterns remained unknown.

Cairns (1987) suggested that variation in the time budgets of marine birds would correlate with prey availability (see also Burger & Piatt 1990, Montevecchi 1993, Monaghan *et al.* 1994). Therefore, study of the foraging patterns of the Antarctic Shag, in conjunction with information on prey availability, could provide qualitative information on fish populations, and may provide an understanding of the relationship between prey availability and the shags' population trend described above. Here we report the foraging patterns observed in the Antarctic Shag at Harmony Point, SSI, throughout the 1995 and 1996 breeding seasons, an aspect of this bird's biology that has received little attention until now.

METHODS

Our study was conducted at Harmony Point (62°17'24"S, 59°13'50"W) (Fig. 1), Nelson Island, SSI, from 28 October 1995 to 16 February 1996 (hereafter 1995 breeding season) and from 27 October 1996 to 21 February 1997 (1996 breeding season).

We acquired 10224 bird-hours of observation—4608 in 1995 and 5616 in 1996—by monitoring 13–18 nests simultaneously during 14 complete days (6 and 8 d in each season, respectively) throughout the breeding seasons. A total of 952 foraging trips were recorded (360 and 592 trips in 1995 and 1996, respectively), noting the time of departure from and return to the colony, and the daily number and duration of foraging trips. Observations were performed “*ad libitum*” (Altmann

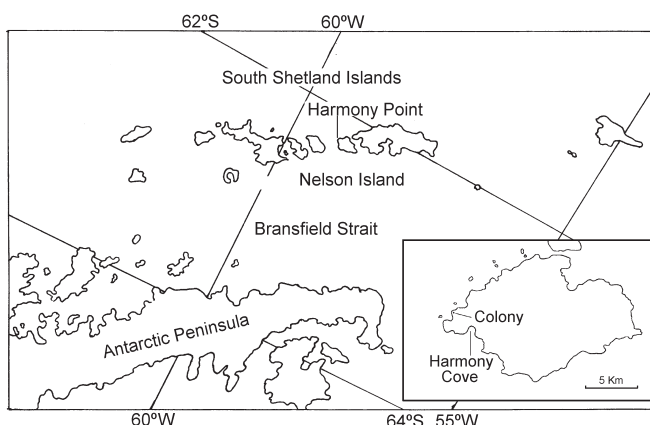


Fig. 1. Location of the study area.

1974) with the naked eye, or using an 8×23 binocular at a distance of 2 and 20 m from the closest and the farthest nests, respectively; we did not detect any reaction of the shags to the presence of the observer.

We also recorded the beginning and ending of foraging activity and the duration of the foraging trips obtained in 1995, during seven observations shorter than 24 h in duration (1 172 bird-h).

TABLE 1
First departure from and last return to the nest according to reproductive status of Antarctic Shags at Harmony Point during the 1995/96 (A) and 1996/97 (B) breeding seasons

A				
	Mean	SD	Range	n
Females pre-laying departure	08h47	02h16	06h08-13h50**	31
Females incubating departure	07h09	01h14	05h53-09h48	23
Females breeding departure	07h45	01h52	05h58-12h46	29
Females overall departure	07h58	01h59	05h53-13h50	83
Males pre-laying departure	14h00	02h29	09h53-19h11	47
Males incubating departure	15h14	01h50	11h07-18h16**	30
Males breeding departure	13h19	02h34	08h37-19h11	34
Males overall departure	14h05	02h22	08h37-19h11	102
Females pre-laying arrival	13h40	03h09	09h00-22h05	31
Females incubating arrival	12h30	02h42	08h13-19h02	23
Females breeding arrival	15h16	02h17	10h05-20h07**	29
Females overall arrival	13h54	02h56	08h13-22h05	83
Males pre-laying arrival	18h06	02h47	11h11-22h54	47
Males incubating arrival	19h34	02h28	11h50-22h40	30
Males breeding arrival	20h07	01h18	16h34-23h03***	34
Males overall arrival	19h00	02h32	11h11-23h03	102
B				
	Mean	SD	Range	n
Females pre-laying departure	07h39	00h43	07h27-10h46	20
Females incubating departure	08h06	01h59	06h48-13h40†	27
Females breeding departure	08h14	02h27	05h27-19h12	66
Females overall departure	08h06	02h08	05h27-19h12	113
Males pre-laying departure	14h04	01h39	11h21-15h59	20
Males incubating departure	14h17	02h07	09h50-20h27†	28
Males breeding departure	12h02	02h19	07h29-18h21**†	67
Males overall departure	12h56	02h24	07h29-20h27	115
Females pre-laying arrival	12h21	01h42	09h26-15h17	20
Females incubating arrival	11h57	02h32	09h30-16h40	27
Females breeding arrival	17h13	03h39	07h58-23h59**†	66
Females overall arrival	15h06	04h00	09h30-23h59	113
Males pre-laying arrival	18h45	02h04	14h05-22h13	20
Males incubating arrival	19h41	02h07	12h31-22h24	28
Males breeding arrival	20h28	01h23	16h41-23h3**	67
Males overall arrival	19h59	01h49	12h31-23h36	115

Asterisks indicates significant inter-reproductive status differences: * P<0.05; ** P<0.01; *** P<0.001. Light cross indicates significant differences between breeding seasons: † P<0.01.

The colony was mapped and the nests numbered. To prevent misidentification of the members of a pair, males were banded on the right leg and females on the left leg. Laying, hatching, and chick dying dates at each nest were recorded every second day during visits to the colony. Therefore, the number of eggs and chicks, and the age of the chicks present at each nest, were known. Times were recorded to the nearest minute using a portable tape-recorder. The time was expressed in local time (3 h behind Greenwich Mean Time). Any trips that were made for bathing (at short distances from the colony) or for collecting nest material, as well as "Circle flights" (*sensu* Van Tets 1965), were recorded as such and were excluded from the analysis. Therefore, in contrast to data gathered by biologging, the information gathered in this study specifically reflects the time that individual birds spent foraging.

RESULTS

In 1995, overall foraging activity took place between 05h53 and 23h03 (Table 1). In 1996, overall foraging was more extended than in the previous season. During this season, males started to forage earlier (Mann-Whitney U-Test (M-W), $P < 0.001$), and individuals of both sexes finished foraging later than in 1995 (M-W, $P < 0.05$ and $P < 0.01$ for females and males, respectively). The period of foraging activity increased throughout the breeding season (Spearman test, $r = 0.89$, $P < 0.0001$ for males, and $r = 0.75$, $P < 0.01$ for females); this was not correlated with the number of daylight hours (Spearman test, ns for both sexes). Whereas the start of foraging activity in females was positively correlated with sunrise (Spearman Test, $r = 0.73$, $P < 0.01$), the end of foraging in males was weakly and not significantly correlated with sunset ($r = 0.11$, ns).

Effect of reproductive status

In 1995, there were differences in the start and end of foraging activity related to the reproductive status of females (Kruskal-Wallis, $F = 5.18$, $P < 0.01$ and $F = 6.59$, $P < 0.01$ respectively) and males ($F = 5.93$, $P < 0.01$ and $F = 8.04$, $P < 0.001$) (Table 1A). Females started foraging significantly later during pre-laying, whereas females with eggs or young finished foraging significantly later. Males started foraging significantly later during incubation, and as the breeding season progressed they finished foraging later.

In 1996, the start of foraging did not vary statistically with the reproductive status of females (Table 1B). However, the end of foraging varied according to reproductive status ($F = 36.07$, $P < 0.01$); breeding females finished foraging activity markedly later than during pre-laying and incubation. Both the start ($F = 13.99$, $P < 0.01$) and end ($F = 8.13$, $P < 0.01$) of foraging varied with the reproductive status of males during the 1996 breeding season. During chick rearing, males started and finished foraging earlier and later, respectively, compared with other periods. Comparison of data between breeding seasons shows that in 1996, incubating females started foraging later (M-W, $P < 0.01$) and rearing females ended foraging later (M-W, $P < 0.001$) than in 1995. In 1996, incubating and rearing males started foraging earlier than in 1995 (M-W, $P < 0.05$ and $P < 0.05$, respectively).

The number of daily foraging trips performed in both seasons by females (1995: $F = 17.70$, $P < 0.01$; 1996: $F = 30.28$, $P < 0.01$) and males (1995: $F = 22.81$, $P < 0.01$; 1996: $F = 35.00$, $P < 0.01$) varied according to reproductive status. For both sexes and seasons, a higher number of

TABLE 2
Variation in the number of daily foraging trips (NDFT), duration of foraging trips (DFT, in min) and daily time spent foraging (DTSF, in min) according to the reproductive status of male and female Antarctic Shags at Harmony Point during the 1995/96 (A) and 1996/97 (B) breeding seasons

A			
	NDFT	DFT (min)	DTSF (min)
Females pre-laying	1.25 ± 0.48 (16)	208.51 ± 126.58 (22)	263.06 ± 104.49 (16)
Females incubating	1.24 ± 0.44 (17)	251.22 ± 131.00 (19)	298.35 ± 138.68 (17)*
Females breeding	2.43 ± 1.03 (31)	118.36 ± 79.79 (73)**	277.55 ± 162.12 (31)**
Male pre-laying	1.25 ± 0.48 (16)	125.07 ± 132.80 (28)	176.75 ± 180.29 (16)**
Males incubating	1.06 ± 0.24 (17)	214.80 ± 128.18 (20)	235.06 ± 128.45 (17)
Males breeding	2.36 ± 0.95 (31)	70.39 ± 56.60 (89)**	191.29 ± 80.59 (31)**
B			
	NDFT	DFT (min)	DTSF (min)
Females pre-laying	1.05 ± 0.22 (20)	262.29 ± 109.74 (21)	275.40 ± 100.05 (20)
Females incubating	1.04 ± 0.19 (29)	223.50 ± 107.98 (30)	231.21 ± 102.17 (29)*
Females breeding	2.72 ± 1.50 (65)	155.18 ± 113.30 (176)**	419.55 ± 174.28 (65)**
Males pre-laying	1.65 ± 0.81 (20)	148.00 ± 139.72 (33)	244.20 ± 133.28 (20)**
Males incubating	1.17 ± 0.38 (29)	269.71 ± 159.89 (34)	316.21 ± 135.74 (29)
Males breeding	3.26 ± 1.51 (65)	121.12 ± 94.36 (211)**	397.05 ± 159.00 (65)**

Abbreviations: NDFT, number of daily foraging trips; DFT, duration of foraging trips; DTSF, daily time spent foraging. Number of observations in parenthesis. Asterisks indicates significant inter-annual differences: * $P < 0.05$; ** $P < 0.01$.

daily foraging trips occurred during the nesting period (N-K, $P < 0.01$) compared with the pre-laying or incubation periods (Table 2).

In both seasons, the duration of foraging trips varied according to the reproductive status of females (1995: $F = 16.88$, $P < 0.01$; 1996: $F = 11.87$, $P < 0.01$) and males (1995: $F = 22.43$, $P < 0.01$; 1996: $F = 26.68$, $P < 0.01$); individuals of both sexes took shorter trips during the chick rearing period (N-K, $P < 0.01$) (Table 2).

Whereas there were no statistical differences in 1995, the time females ($F = 19.06$, $P < 0.01$) and males ($F = 9.00$, $P < 0.01$) spent away from the colony in 1996 varied throughout the breeding season (Table 2). Individuals of both sexes spent more time foraging when they were rearing chicks (N-K, $P < 0.05$), and less time foraging during the pre-laying and incubation periods (Table 2).

There were no statistical differences between seasons in the number of daily foraging trips performed by males and females having the same reproductive status (Table 2). The duration of foraging trips of chick-feeding individuals in 1995 was shorter than in 1996 (M-W, $P < 0.01$ for both sexes). Whereas in 1995 incubating females spent more time foraging than in 1996 (M-W, $P < 0.05$), in 1996, pre-laying males and chick-feeding males and females spent more time foraging than in the previous season (M-W, $P < 0.01$ for both sexes).

Effect of brood size

The number of daily foraging trips performed by females in 1996 ($F = 4.36$, $P < 0.05$) and by males in both seasons (1995: $F = 8.30$, $P < 0.01$; 1996: $F = 5.94$, $P < 0.01$) varied according to the number of chicks at the nest (Table 3). As expected, except for males rearing two chicks in 1995, the highest number of daily foraging trips was observed in individuals rearing three chicks (N-K, $P < 0.05$). In 1995, gender differences in the number of daily foraging trips were only statistically significant between females and males rearing three chicks (M-W, $P < 0.05$). In 1996, males rearing one chick foraged more frequently than their partners (M-W, $P < 0.05$). Compared to 1995, in 1996, males displayed more daily foraging trips ($F = 8.30$, $P < 0.01$), with differences in males rearing one (N-K, $P < 0.05$) and three chicks (N-K, $P < 0.05$) being statistically significant.

Although no trend was observed in 1995, the duration of foraging trips performed in 1996 by females ($F = 7.02$, $P < 0.01$) and males ($F = 5.58$, $P < 0.01$) decreased as the number of chicks at the nest increased. Except in pairs with one chick in 1995, males with one, two, and three chicks performed foraging trips that were significantly shorter in duration than their partners (M-W, $P < 0.05$) in both seasons.

The daily time spent foraging did not increase significantly with the number of chicks at the nest. In 1995, females with two (M-W, $P < 0.01$) and three chicks (M-W, $P < 0.05$) invested more time in foraging activities than their partners. The differences observed in 1996 were not statistically significant. The daily time spent foraging by females ($F = 10.26$, $P < 0.01$) and males ($F = 31.78$, $P < 0.01$) was remarkably different in both seasons. In 1996, females rearing one (N-K, $P < 0.05$) and two chicks (N-K, $P < 0.05$), and males rearing one (N-K, $P < 0.01$), two (N-K, $P < 0.001$), and three (N-K, $P < 0.05$) chicks, spent more time foraging than in the previous season.

Effect of chick growth

The number of daily foraging trips displayed by males rearing one chick (Spearman test, $r = 0.81$, $P < 0.01$), and by females ($r = 0.57$, $P < 0.05$) and males ($r = 0.61$, $P < 0.05$) rearing two chicks, increased as chicks grew older in 1995. In 1996, that trend was statistically significant in males ($r = 0.42$, $P < 0.05$) rearing one chick, in females ($r = 0.44$, $P < 0.05$) and males ($r = 0.43$, $P < 0.05$) rearing two chicks, and in females rearing three chicks ($r = 0.64$, $P < 0.05$).

In both seasons, the duration of foraging trips was weakly (and not significantly) correlated with chick age in nests with one, two, and three chicks.

Although the daily time females and males spent foraging tended to increase as chicks grew older in 1995, this trend was only statistically significant in females rearing two chicks ($r = 0.75$, $P < 0.01$). Interestingly, this trend was also significant ($r = 0.99$, $P < 0.05$) in a male whose partner abandoned the colony and who successfully reared the only chick at the nest. In 1996, except for males rearing three chicks, the daily time females and males spent

TABLE 3
Variation in the number of daily foraging trips, duration of foraging trips, and daily time spent foraging according to brood size in Antarctic Shags at Harmony Point during the 1995/96 (A) and 1996/97 (B) breeding seasons

A	1 chick			2 chicks			3 chicks		
	NDFT	DFT (min)	DTSF (min)	NDFT	DFT (min)	DTSF (min)	NDFT	DFT (min)	DTSF (min)
Females	1.9 ± 1.0	98.8 ± 100.5	211.4 ± 160.6	2.5 ± 0.9	115.0 ± 84.1*	312.4 ± 65.7**	3.5 ± 0.6*	100.0 ± 38.5*	370.5 ± 31.6*
Males	1.7 ± 0.7	56.9 ± 68.5	161.4 ± 86.5	2.9 ± 1.0	55.5 ± 43.9*	214.1 ± 73.5**	2.3 ± 0.5*	56.8 ± 55.7*	208.5 ± 70.0*
Pairs	3.2 ± 1.2	73.0 ± 84.1	372.8 ± 190.3	5.4 ± 1.3	79.3 ± 69.2	515.6 ± 128.6	5.8 ± 0.5	77.0 ± 52.4	579.0 ± 86.0
B	1 chick			2 chicks			3 chicks		
	NDFT	DFT (min)	DTSF (min)	NDFT	DFT (min)	DTSF (min)	NDFT	DFT (min)	DTSF (min)
Females	1.9 ± 1.0*	197.4 ± 127.6*	386.1 ± 142.2	3.0 ± 1.4	142.1 ± 113.7*	435.4 ± 186.7	4.0 ± 1.7	111.8 ± 75.6*	457.6 ± 221.0
Males	2.6 ± 1.0*	137.3 ± 105.0*	380.6 ± 144.1	3.2 ± 1.3	113.9 ± 97.2*	400.8 ± 184.2	5.0 ± 1.8	80.1 ± 64.6*	421.2 ± 133.7
Pairs	4.5 ± 1.5	162.1 ± 118.1	766.7 ± 260.8	6.2 ± 2.1	127.1 ± 105.9	839.5 ± 325.4	9.0 ± 3.1	93.9 ± 71.0	858.8 ± 328.2

Abbreviations: NDFT, number of daily foraging trips; DFT, duration of foraging trips; DTSF, daily time spent foraging.

Asterisks indicates significant gender differences: * $P < 0.05$; ** $P < 0.01$.

foraging increased significantly with the age of the chicks in nests with one, two, and three chicks ($r > 0.58$, $P < 0.01$).

As expected, when data from both seasons were combined, we realized that the daily number of foraging trips increased with chick age in pairs rearing one (Spearman test, $r = 0.57$, $P < 0.01$), two ($r = 0.68$, $P < 0.0001$), and three ($r = 0.78$, $P < 0.001$) chicks (Fig. 2). The daily time spent foraging by pairs rearing one (Spearman test, $r = 0.70$, $P < 0.0001$), two ($r = 0.77$, $P < 0.0001$), and three ($r = 0.81$, $P < 0.0001$) chicks also increased with chick age (Fig. 3).

DISCUSSION

As observed in some other shag species (Shaw 1986, Platteeuw & Van Eerden 1995, Wanless *et al.* 1995), each member of an Antarctic Shag pair foraged once a day during pre-laying, incubation, and early chick rearing. Females usually did so early in the morning, as did males upon return of their partners—but only after several trips gathering nest material. Similar to what has been reported for *P. pelagicus* and *P. penicillatus* (Ainley *et al.* 1990), as well as

P. carbo (Grémillet 1997) and *P. melanogenis* (Cook *et al.* 2007), as Antarctic Shag chicks grew older and the energy requirements at the nest increased, their parents increased the number of foraging trips, usually alternating the time at sea. Except in 15 cases (1.8%), the first trip was performed by females and the last one by males, which has also been reported by Bernstein & Maxson (1984) and Favero *et al.* (1998). This very strict pattern was occasionally altered on foggy or stormy days, or by pairs rearing three large chicks. This pattern might be also influenced by the feeding performance of individuals during the previous or current day. Perhaps due to a lack of time to cover the energy requirements at the nest, and/or the low availability of food near the colony, the Antarctic Shag at the SSI displayed behaviors that tended to diminish intraspecific competition (Casaux *et al.* 2001) and/or enhance breeding output. According to Bernstein & Maxson (1984), this behavior may have influenced the gender divergence in foraging times. Once this pattern is established, it might be expected that those individuals that do not follow the “rules” will struggle to raise their chicks successfully. During nest building, pre-laying, incubation, and early rearing, males foraging during the “females’ time” leave their nests

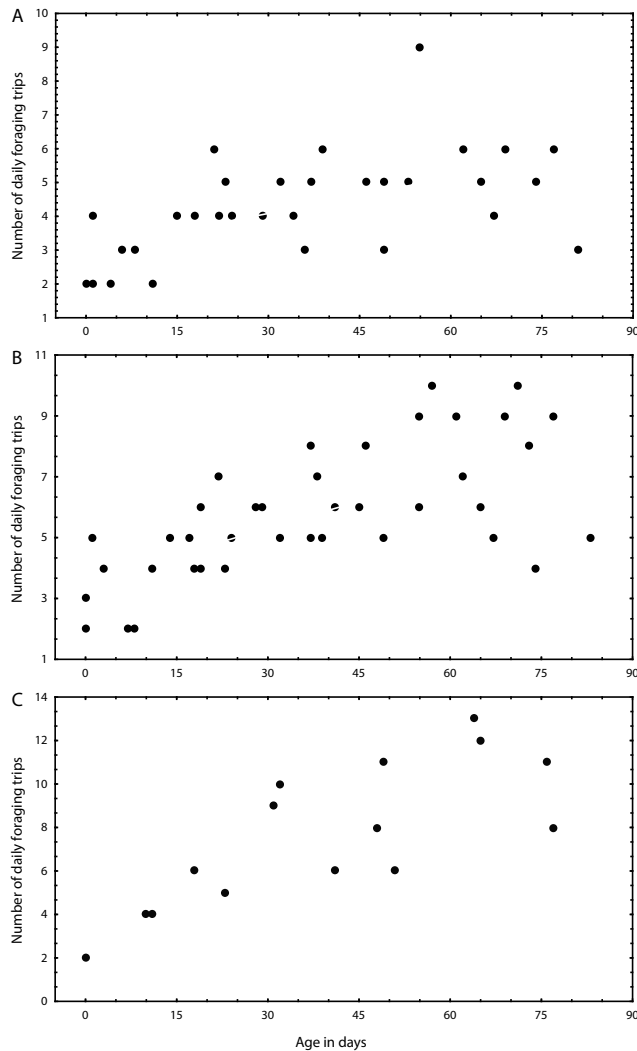


Fig. 2. Variation in the daily number of foraging trips performed by pairs of Antarctic Shag at Harmony Point during the 1995/96 and 1996/97 breeding seasons according to chick age in broods of 1 (A), 2 (B) and 3 (C) chicks.

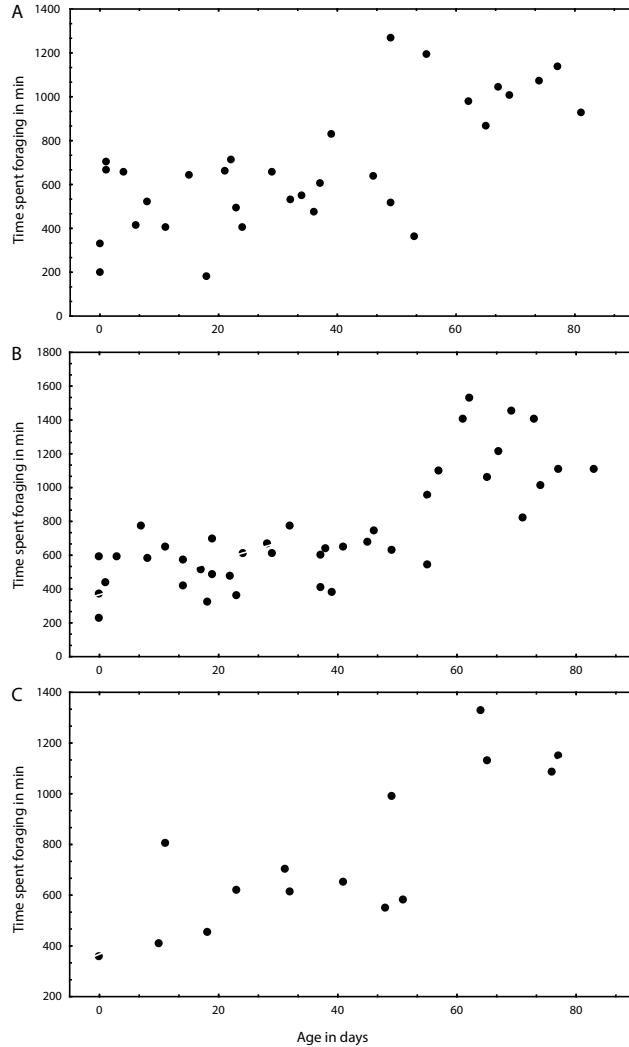


Fig. 3. Variation in the daily time spent foraging by pairs of Antarctic Shag at Harmony Point during the 1995/96 and 1996/97 breeding seasons according to chick age in broods of 1 (A), 2 (B) and 3 (C) chicks.

exposed to nest material thievery or loss of eggs/chicks because of the low level of aggression in their female partners who are limited in their ability to defend against attacks from the other males. On the other hand, females foraging during the “males’ time” must compete for food with other males who are more powerful and more skilled at diving and prey handling. However, in our observations, we did not find any evidence for negative consequences of an altered foraging pattern. During mid- and late-chick rearing, when chicks can thermoregulate on their own and are safe from predation, partners usually take several daily foraging trips, alternating their time at the nest, implying that males and females from different nests forage simultaneously. Therefore, the sexual segregation in foraging areas/depths, and/or in diet, is required to diminish competition between genders. In fact, at Harmony Point, Casaux *et al.* (2001) provided evidence for gender differences in diving depths and in the composition of diet; they also found preliminary evidence for sexual differences in the use of foraging areas.

As in other shags (Ainley *et al.* 1990, Williams *et al.* 1991, Wanless *et al.* 1995, 1999), the Antarctic Shag forages during daylight hours. The period of foraging activity varied throughout the season, mainly in relation to energy requirements at the nest. However, the start of foraging activity in females was positively correlated with sunrise (Bernstein & Maxson 1984). Since the main fish prey of the Antarctic Shag inhabit coastal waters year-round (Casaux *et al.* 1990), it might be advantageous to align the higher energy requirements of nesting with the period of maximum daylight hours. This would allow individuals to avoid any “bottle-neck” that would occur when attempting to feed older chicks during shorter days, when it would be impossible to sufficiently increase the number of daily foraging trips. However, different factors—such as the presence of pack-ice around the colony or cover of the nesting area in snow—can delay the start of breeding activities. Compared to 1995, the pairs in 1996 better synchronized both variables—laying their eggs early—but then suffered higher chick mortality and fledged lighter chicks (see below). This provides evidence that factors other than synchronicity between the daylight cycle and nesting requirements can strongly influence the breeding output of these birds.

As observed in *P. c. sinensis* in the Netherlands (Platteeuw & Van Eerden 1995), in *P. melanogenis* at Crozet Island (Cook *et al.* 2007), and in the Antarctic Shag at the Antarctic Peninsula and the SSI (Bernstein & Maxson 1985, Favero *et al.* 1998, respectively), although both sexes displayed a similar number of daily foraging trips, females spent more daily time foraging (Tables 2 and 3). It is thought that female *P. c. sinensis* start to forage earlier and spend more daily time foraging because their feeding areas are located farther from the colony (Platteeuw & Van Eerden 1995). Diamond (1974) proposed that to compensate for the longer trips, female Red-footed Boobies *Sula sula* digest part of the food load at the feeding area, a behavior that cannot be confirmed for the Antarctic Shag. In contrast to the foraging habits of *P. c. sinensis* reported by Platteeuw & Van Eerden (1995), Casaux *et al.* (2004) observed that female Antarctic Shags at Harmony Point use foraging areas located closer to the colony. On the other hand, male Antarctic Shags provide more food to their young than females (even when the mass of the individuals is accounted for) (Favero *et al.* 1998), a finding that invalidates the hypothesis that females invest more time in foraging activities due to a higher breeding effort. Several factors may explain the gender differences in the daily time spent foraging, such as temporal differences in prey availability (Casaux *et al.* 2001), differences between males and females in how they

spend their time at sea, or the greater difficulty that females have in meeting the foraging expectations of commuting trips (e.g., because they forage deeper on prey that is smaller than that obtained by males [Casaux *et al.* 2001]).

Compared to the egg stage of nesting, in 1995, males and females rearing chicks increased their number of foraging trips but diminished their daily time spent at sea (Table 2). Because the energy requirements at the nest during chick provisioning are remarkably higher than during incubation, this decrease in the time spent foraging suggests that individuals may have optimized their foraging trips. This could be accomplished through a higher prey catch rate and/or by reducing the time invested in non-essential foraging activities (i.e., inter-diving bout resting periods, swimming, or resting on the sea surface, etc.), therefore buffering variable food abundance or energy requirements (Burger & Piatt 1990). Conversely, in 1996, the daily time spent foraging during chick provisioning was longer than during incubation (Table 2). This increase in foraging effort might reflect greater difficulties in covering the energy requirements in 1996 (see below), and might indicate that the ability to buffer variations in food abundance was exceeded. As the energy requirements at the nest increased (as chicks grew in number and age), parents increased the number of foraging trips and time spent foraging, while at the same time reducing trip duration (which supports the existence of “buffer activities”). During this time, birds likely optimized their time at sea and/or improved their prey catch rate (Table 3). Because shags forage during daylight hours, in those areas/seasons when food availability is inadequate in quantity or distance, a “bottle-neck” may occur as a consequence of being unable to sufficiently increase the number of feeding trips. If an unavoidable food provisioning limit for chicks exists, it is impossible to raise all of the chicks successfully. In 1996, shags spent more time foraging, foraged more frequently, and dove significantly longer and slightly deeper (Casaux 2004), which correlated with higher chick mortality ($\chi^2_1 = 5.38$, $P < 0.05$) and lighter fledglings than in 1995 (males: 3 161.5 g in 1995 and 3 092.6 g in 1996, M-W, ns; females: 2 900.9 g in 1995 and 2 681.0 g in 1996, $P < 0.05$; RC, unpubl. data). Such a difference might be explained by lower food availability in the foraging areas. Therefore, despite the increase in energy expended on foraging in 1996, Antarctic shags were unable to fully compensate for the presumed reduction in food availability, supporting the idea of limits in provisioning as stated above. In agreement with this hypothesis, Ainley *et al.* (1990) observed shorter and more frequent trips among Brandt’s and Pelagic cormorants at the Farallon Islands in years when food was more abundant, closer to the colony, and more chicks were raised.

The Antarctic Shag diet is thought to reflect qualitative changes in the littoral fish community (CCAMLR 2003). As described above, variation in time budgets of marine birds correlates with prey availability (Cairns 1987, Burger & Piatt 1990, Ainley & Boekelheide 1990, Montevecchi 1993, Monaghan *et al.* 1994). Based on our results, we suggest that some of the foraging parameters of the Antarctic Shag considered here (i.e., daily number of feeding trips and the daily time invested in foraging), as well as some reproductive and population parameters, do reflect changes in food availability. These findings can be applied to programs that monitor trends in Antarctic littoral fish populations. However, the shag populations studied here display activities that can buffer variable food abundance or energy requirements. As a result, in agreement with Burger & Piatt (1990), before using foraging parameters in assessing changes in food availability, the role of flexible time budgets must be clarified.

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