

THE DIET OF THE ANTARCTIC SHAG DURING SUMMER AT NELSON ISLAND, ANTARCTICA¹

MARCO FAVERO

Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales,
Departamento de Biología, Funes 3250, (7600) Mar del Plata, Argentina,
e-mail: mafavero@mdp.edu.ar

RICARDO CASAUX

Instituto Antártico Argentino, División Biología, Cerrito 1248, (1010) Buenos Aires, Argentina

PATRICIA SILVA

CIC–Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales,
Departamento de Ciencias Marinas, Funes 3350, (7600) Mar del Plata, Argentina

ESTEBAN BARRERA-ORO AND NESTOR CORIA

Instituto Antártico Argentino, División Biología, Cerrito 1248, (1010) Buenos Aires, Argentina

Abstract. Analysis of 139 stomach contents of the Antarctic Shag (*Phalacrocorax bransfieldensis*) collected at Nelson Island, Antarctica, showed that fish were the main component in the diet, followed by octopods, gammarids, euphausiids, and polychaetes. The fish *Nothothenia coriiceps* predominated in frequency (56%) and in mass (49%), whereas *Harpagifer antarcticus* was the most important by number (58%). The sizes of *N. coriiceps* and *H. antarcticus* taken by males were significantly larger than those caught by females. This dietary difference is probably due to differential prey selection related to shags' sexual dimorphism, temporal prey availability, and/or different foraging depths/areas. Observations at nests showed that females mainly foraged in the morning, whereas males foraged in the evening. No significant differences were observed between the number of daily foraging trips made by males and females, averaging 1.7 during incubation, 2.0 in early chick-rearing, and 4.6 during the late chick-rearing period. The estimated daily food intakes were 321, 315, and 758 g for females, and 421, 582, and 1,288 g for males during incubation, early and late chick-rearing, respectively.

Key words: Antarctic Shag, Antarctica, diet, fish, *Phalacrocorax bransfieldensis*, prey temporal variation, sexual variation in foraging.

INTRODUCTION

The Antarctic Shag (*Phalacrocorax bransfieldensis*) is distributed in the Antarctic Peninsula and South Shetland Islands (del Hoyo et al. 1992), and feeds predominately on demersal benthic fish (Casaux and Barrera-Oro 1993, Coria et al. 1995) close inshore at depths to 116 m (Croxall et al. 1991). The diet of shags has been studied mainly by analysis of regurgitated casts (Green et al. 1990a, 1990b, Barrera-Oro and Casaux 1996). Although this method provides useful information with minimal disturbance and sampling effort, the erosion by digestion and loss of otoliths and other hard parts throughout the gastrointestinal tract could give biased results, a fact largely proved in trials with captive cormorants (Casaux et al. 1995b, Zijlstra and Van Eerden 1995), or by comparison between

regurgitations and pellets (Casaux et al. 1995a, Veldkamp 1995). On the other hand, analysis of stomach contents can stress the birds, demands more time in the field, and must be used with caution when inferring meal sizes (Duffy and Jackson 1986). However, it gives better information on the size and mass of prey items, and permits inferences about the foraging behavior and energy requirements of birds. Coria et al. (1995) provided information on the diet of Antarctic Shags at the South Shetland Islands by analysis of stomach contents, but the data were restricted to the middle chick-rearing period.

There is a paucity of information on sexual variation in the diet of this species. Bernstein and Maxson (1984) at Anvers Island observed sexual differences in time budget and feeding/diving behavior of Antarctic Shags, thus suggesting the possibility of a diet composed of different size and/or species of prey as reported for King Cormorants (*Phalacrocorax albiventer*) at

¹ Received 10 October 1996. Accepted 17 October 1997.

Macquarie Island (Kato et al. 1995). A similar situation was found by Kato et al. (1991) and Wanless et al. (1995) for South Georgia Shags (*P. georgianus*) at South Georgia Islands.

Here we provide information on the diet of Antarctic Shag, analyzing sexual differences and variation throughout different stages of the breeding season, as well as foraging activity and consumption rates. We adopted the nomenclature of Antarctic Shag (*Phalacrocorax bransfieldensis*, formerly Blue-eyed Shag *P. atriceps bransfieldensis*) following the revisions given in Marchant and Higgins (1990) and del Hoyo et al. (1992).

METHODS

We collected 139 stomach contents of the Antarctic Shag from 1 December 1994 to 2 February 1995 at Duthoit Point (62°18'S, 58°47'W), Nelson Island, South Shetland Islands, Antarctica. Samples were obtained from breeding birds just returning to the colony from foraging trips, and captured at the nests with hand nets. Stomach contents were obtained applying the "shaking" technique, which consisted of a brief shake of a shag to induce regurgitation (Cooper 1985a). This shaking induces complete regurgitation (Coria et al. 1995).

Samples were taken in three periods of three days each: period 1 from 1 to 3 December 1994 (during incubation, $n = 46$), period 2 from 22 to 24 December 1994 (early rearing, $n = 46$), and period 3 from 31 January to 2 February 1995 (late rearing, $n = 47$). During the second period, chick body mass averaged (\pm SE) 288 \pm 55 g ($n = 52$), which corresponds to approximately 9 days of age (range 6–11 days); during the third period, chicks averaged 2,683 \pm 73 g ($n = 40$), equivalent to 42 days of age (range 35–53 days). Age was estimated using unpublished data from M. Favero, and Coria et al. (1995).

Sexual and daily activity patterns were taken into account, and each sampling day was divided into three blocks: (1) 08:00 to 12:00, (2) 13:00 to 17:00, and (3) 18:00 to 22:00 local time (+3 GMT). No samples were taken during the rest of the day because during those hours the behavior of shags mainly was restricted to resting at the colony. Nests were plotted to ensure that in each sampling period, one sample represented one bird. A minimum of five stomach contents was collected per block of time. Birds were

sexed by comparing body weight, bill length, and vocalizations between members of a pair, assuming that males (3,202 \pm 247 g and 56.0 \pm 1.3 mm, respectively) were larger than females (2,768 \pm 121 g, 52.8 \pm 1.7 mm, respectively) (Bernstein and Maxson 1985).

Samples from stomach contents were weighed, sorted into alimentary items, and total length (TL, to 0.1 cm) and mass (g) of fish were recorded. When fish specimens were digested (7% of 1,019 fish obtained), the otoliths were recovered, identified, and measured to calculate their size and mass (Hetch 1987, Casaux and Barrera-Oro 1993).

To estimate foraging rate, each sampling period was complemented with one day of continuous observation of 5–7 nests located in an undisturbed area of the colony. A total of 864 bird hours (336, 288, and 240 in the three periods, respectively) was obtained, and 94 foraging trips were recorded. During the incubation and early rearing periods, the average duration of the trips were used to distinguish foraging (170 min, $n = 24$, and 126 min, $n = 24$, respectively) from other trips where shags were usually observed bathing or collecting nest material in shallow waters (7 min, $n = 33$, and 10 min, $n = 16$, respectively). In the late chick-rearing period, a foraging trip was assumed when the adults returned to the nest and immediately fed their chicks.

RESULTS

The mean mass (\pm SE) of the stomach contents was 219.6 \pm 10.4 g (range 16–540 g, $n = 139$), and no significant differences ($F_{2,131} = 0.5$, $P > 0.50$) were found between sampling periods (207, 231, and 221 g during incubation, early chick-rearing, and late chick-rearing, respectively). The mean mass of the loads from males (268.3 \pm 15.7 g, $n = 69$) and females (172.3 \pm 11.2 g, $n = 70$) differed significantly ($t_{137} = 5.0$, $P < 0.001$). Fish were present in every sample and were the most important prey, followed by octopods (*Pareledone charcoti*), gammarids (mainly *Bovallia gigantea*), euphausiids (*Euphausia superba*), and polychaetes (nereids) (Table 1). No significant differences were found in the occurrence of prey items through the three sampling periods ($\chi^2_2 = 1.3$, $P > 0.50$), and shags fed almost exclusively on fish during the entire breeding season (Table 1). Other prey were more important in females (Table 2).

TABLE 1. The composition of the diet of Antarctic Shags at Duthoit Point during summer 1994–1995, as observed throughout different stages of the breeding season ($n = 139$). Only stages where the food item was found are shown.

	% of samples (occurrence)	Number of prey	% number	Mass (g)	% mass
Fish					
Incubation	100.0	334	87.4	9,816	97.4
Early rearing	100.0	328	89.1	9,455	97.6
Late rearing	100.0	350	97.8	10,423	98.4
Octopods					
Incubation	12.5	12	3.1	220	2.2
Early rearing	8.7	5	1.4	190	2.0
Late rearing	13.0	8	2.2	170	1.6
Polychaetes					
Early rearing	2.2	1	0.3	2	0.0
Gammarids					
Incubation	20.8	33	8.6	36	0.4
Early rearing	21.7	28	7.6	29	0.3
Euphausiids					
Early rearing	10.9	6	1.6	6	0.1
Stones					
Incubation	2.1	3	0.8	5	0.0

A total of 1,019 fish were represented in the samples, belonging to 8 species: *Notothenia coriiceps*, *Lepidonotothen nudifrons*, *Harpagifer antarcticus*, *Trematomus newnesi*, *Gobionotothen gibberifrons*, *Notothenia rossii*, *Pagothenia bernacchii*, and *Parachaenichthys charcoti*. Nine fish prey remained unidentified. *N. coriiceps* was the most frequent (F% [occurrence] = 56.1) and important in mass (48.5%), whereas *H. antarcticus* predominated in number (57.6%), more so in females (560) than in males (23).

The mean number of fish per sample was 7.4 (range 1–34), and no significant differences were observed between periods ($F_{2,135} = 0.1$). The differences were significant in the comparison between sexes ($t_{137} = 7.0$, $P < 0.001$) being 11.1 ± 0.9 ($n = 70$) for females and 3.6 ± 0.4 ($n = 69$) for males. Seventy-seven stomach samples (55%) were composed of a single fish species, 41 of them were *N. coriiceps*. In 32 samples (23%) a single specimen was found, 29 of them were *N. coriiceps*.

The size of several fish species, including *N. coriiceps*, *H. antarcticus*, *N. nudifrons*, and *T. newnesi* varied significantly throughout the sampling periods (all $P < 0.05$). *Harpagifer antar-*

ticus and *P. charcoti* predominated in female diet, whereas *T. newnesi* was mainly eaten by males. The average size (\pm SE) of the *N. coriiceps* and *H. antarcticus* specimens ingested by males (23.4 ± 0.7 and 7.7 ± 0.2 cm, respectively) was significantly larger ($t_{76} = 7.0$, $P < 0.001$; $t_{531} = 2.5$, $P < 0.05$, respectively) than those ingested by females (15.7 ± 0.8 and 7.1 ± 0.1 cm, respectively). No significant differences were observed between *L. nudifrons* ($t_{199} = 0.2$) and *T. newnesi* ($t_{82} = 0.3$) foraged by males and females (Fig. 1). In addition, no significant differences were observed within sexes in the comparison of fish sizes caught throughout the three sampling periods (one-way ANOVA, $P > 0.05$ for both sexes).

No significant differences were observed between males and females in the number of foraging trips per day made during the three sampling periods (t -test, $P > 0.5$ in all comparisons). Shags averaged 1.7 ± 0.2 ($n = 14$) trips bird⁻¹ day⁻¹ during incubation, 2.0 ± 0.3 ($n = 12$) in early rearing, and 4.6 ± 0.5 ($n = 10$) in late rearing (Kruskal-Wallis test, $\chi^2_2 = 23.2$, $P < 0.001$). The foraging activity started from 06:00 to 07:15 and finished from 20:00 to 21:30; females mainly foraged in the morning (71% of the trips), whereas males foraged in the evening

TABLE 2. Sexual differences in the diet of Antarctic Shags at Duthoit Point during summer 1994–1995.

	Females (n = 70)	Males (n = 69)	Total
Fish			
% Frequency	100.0	100.0	100.0
Number	760	252	1,012
% Number	75.1	24.9	91.3
Octopods			
% Frequency	21.4	1.4	11.5
Number	24	1	25
% Number	96.0	4.0	2.3
Polychaetes			
% Frequency	1.4	0.0	0.7
Number	1	0	1
% Number	100.0	0.0	0.1
Gammarids			
% Frequency	15.4	4.3	14.4
Number	49	12	61
% Number	80.3	19.7	5.5
Euphausiids			
% Frequency	5.7	1.4	3.6
Number	5	1	6
% Number	83.3	16.7	0.5

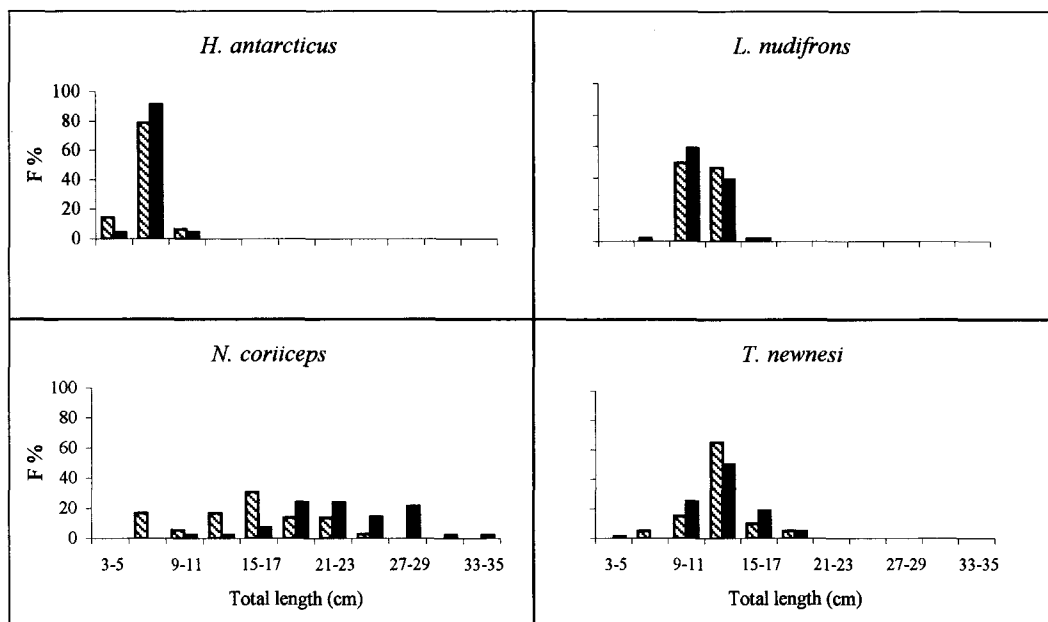


FIGURE 1. The percent frequency distribution (F%) by length of the fish prey species caught by males (solid bars) and females (hatched bars) of the Antarctic Shag at Duthoit Point during summer 1994–1995.

(44%). The duration of the trips differed significantly throughout the season, averaging 173, 126, and 91 min during the incubation, early and late chick-rearing periods, respectively ($F_{2,71} = 6.0$, $P < 0.01$). The time spent away averaged 150 ± 17 min ($n = 28$) in males and 129 ± 17 min ($n = 32$) in females ($t_{38} = 0.9$).

Using the mean mass of the stomach contents by sex during the three sampling periods, and the mean number of daily foraging trips, the average daily intake ranged from 421 to 1,288 g for males, and from 321 to 758 g for females. Assuming that fish represents 98% of the shags' diet and that fish provide an energy content of 3.97 kJ g^{-1} (Croxall et al. 1985) and an assimilation efficiency of 75% (Wiens 1984), we estimated an averaged intake of 1,941 and 1,383 kJ day^{-1} for males and females, respectively.

DISCUSSION

As reported in previous diet studies based upon the analysis of pellets (Casaux and Barrera-Oro 1993, Barrera-Oro and Casaux 1996), our results indicated that fish were the main prey of the Antarctic Shag. Mollusks were the next most common prey, which agrees with other studies carried out in the same area (Casaux and Barrera-Oro 1993, Coria et al. 1995).

Coria et al. (1995), also at Duthoit Point but in a previous season, reported that the foraging activity of Antarctic Shags was restricted to daylight hours. In agreement with previous studies carried out in the Antarctic Peninsula (Bernstein and Maxson 1984) and South Georgia Islands (Kato et al. 1991, Wanless et al. 1995), females mainly foraged in the morning, whereas males were more active during the rest of the day. As reported by Kato et al. (1995) on Macquarie shags (*P. purpurascens*) in sub-Antarctica, Antarctic Shag males brought back heavier loads composed of a few large fish, whereas females brought back lighter loads made up of a larger number of small prey items.

SEXUAL DIFFERENCES IN THE DIET

Although the fish species ingested by both sexes were similar, some differences were observed; males preyed on larger fish (e.g., *N. coriiceps* and *H. antarcticus*) than did females (Fig. 1). These differences in prey choice could be related to (1) sexual size dimorphism, (2) temporal prey availability, given that males and females differentially distributed their foraging effort during the day, and/or (3) sexual differences in diving depths or foraging areas. Hypothesis (1) is supported by the fact that females, which are

up to 20% lighter than males, preyed mainly on smaller fish. However, the largest *H. antarcticus* specimens, which were ingested by males, were smaller than the *N. coriiceps* specimens eaten by females. In support of hypothesis (2), Casaux et al. (1990) observed at Potter Cove (10 km from Duthoit Point) that activity of adult *N. coriiceps* was infrequent during the morning and increased in the afternoon/evening, which coincided with male foraging activity. Regarding hypothesis (3), it has been suggested for cormorants that, due to the higher functional body oxygen stored, larger species display deeper dives (Cooper 1986). Therefore, sexual differences in diving depths and/or behavior are expected. In Potter Cove (King George Island), larger *N. coriiceps* specimens inhabit deeper waters (R. Casaux, unpubl. data), and it is probable that at Duthoit Point, the Antarctic Shag partitioned the use of the foraging depths and/or areas with males preying in deeper waters than did females, thus diminishing intraspecific competition.

Sexual differences in diet also have been recorded in other Antarctic birds (Volkman et al. 1980, Croxall and Lishman 1987). Clarke et al. (1995) suggested that such differences in Adeline Penguins *Pygoscelis adeliae* may become important as a means of reducing intraspecific competition and of maximizing the chances of one member of the pair locating food for the chicks without excessive waste of overall search effort. Despite substantial differences in the timing and pattern of diving between sexes of South Georgia Shags at Bird Island (South Georgia Islands), no definitive difference in diving depths between male and female birds has been observed (Kato et al. 1991).

CONSUMPTION RATES

The daily food requirement for the Antarctic Shag is reported to range from 600 to 1,209 g (Shaw 1984). Coria et al. (1995), while studying the same species during the middle rearing period (chicks averaging 1,400 g and 22 days of age), obtained a maximum daily intake of 1,410 g. The range of daily food intake estimated for each period in this study was greater than previous work. The variation through the chick rearing period can be explained by the increase in the chicks' energy demand. Although food loads remain constant, adults respond to that demand by increasing the number of foraging trips and the time spent away, which is similar to the

findings of Bernstein and Maxson (1985) at Anvers Island. In contrast, Wanless et al. (1995) found no evidence that the number of trips and the time spent foraging increased with chick age at Bird Island. South Georgian Shags probably respond to the growing chicks' energy demands by increasing the mass of the food loads and/or foraging on more energetically rich prey. On the other hand, some differences were reported in other cormorants regarding the number and duration of foraging bouts by males and females. In the Bank Cormorant (*Phalacrocorax neglectus*), female foraging bouts are longer than that of males, whereas males showed significantly more foraging bouts than did females (Cooper 1985b). However, our data indicate that both sexes distributed similarly their foraging effort, at least considering the time spent away and the number of foraging trips performed during the incubation and chick-rearing period.

Considering the food loads for each sex and that there were no differences between the sexes in the number of foraging trips, males brought a greater amount of food to the nests. The energy intake differed by 24, 46, and 42% between sexes during incubation, early and late chick-rearing, respectively, which was higher than the 15% estimated by Bernstein and Maxson (1985) at the Antarctic Peninsula by means of activity budget. The difference in energy intake between sexes also occurred during the incubation period, indicating that it cannot be solely attributed to a simple difference in chick provisioning.

The energetic estimations for incubating (2,384 and 2,754 kJ bird⁻¹) and early rearing (2,330 and 2,688 kJ bird⁻¹) Antarctic Shags (females and males, respectively) represent about half of the daily energy expenditures calculated by means of time budget estimations of Bernstein and Maxson (1985). The differences observed between our values and those from the literature could be due to limitations of the methodology used in this work: (a) biases during this study in the estimation of the mean number of foraging trips; when the maximum numbers of observed trips were tested, our values for incubating and early chick-rearing fall into the range reported by Bernstein and Maxson (1985); and/or (b) biases in the estimation of the food ingested per trip; Wanless et al. (1993) postulated that breeding *Phalacrocorax aristotelis* digest their own food before returning to the nest and the contents of the loads were primarily for the

chicks. During our study, adult shags were frequently observed resting in the foraging area between dives for periods longer than 1 hr. Moreover, the digested remains found in regurgitations could contribute, at least partially, to adult requirements. On the other hand, our estimations for the third period (3,834 and 2,257 kJ day⁻¹ bird⁻¹ for males and females, respectively) fit better with the energy expenditure for late rearing shags (2,844 and 2,443 kJ day⁻¹ bird⁻¹ for males and females, respectively) reported by Bernstein and Maxson (1985).

These findings suggest that more detailed studies on the foraging behavior of the Antarctic Shag are needed. Further knowledge of the energetic cost of adults foraging for chicks, their meal size and feeding frequency should allow more precise estimates of total adult energy expenditure during the chick-rearing period, particularly taking into account sexual differences.

ACKNOWLEDGMENTS

We thank C. Bellisio for his assistance in part of the field work, and M. Rovetta for his logistic support. J. Cooper made helpful comments on an earlier draft. We also thank S. J. Maxson, W. D. Koenig, and two anonymous referees whose criticisms improved the manuscript.

LITERATURE CITED

- BARRERA-ORO, E., AND R. J. CASAUX. 1996. Fish as diet of the Blue-eyed Shag *Phalacrocorax atriceps bransfieldensis* at Halfmoon Island, South Shetland Islands. *Cybiurn* 20:37-45.
- BERNSTEIN, N. P., AND S. J. MAXSON. 1984. Sexually distinct daily activity patterns of Blue-eyed Shags in Antarctica. *Condor* 86:151-156.
- BERNSTEIN, N. P., AND S. J. MAXSON. 1985. Reproductive energetics of Blue-eyed Shags in Antarctica. *Wilson Bull.* 97:450-462.
- CASAUX, R., AND E. BARRERA-ORO. 1993. The diet of the Blue-eyed Shag, *Phalacrocorax atriceps bransfieldensis* feeding in the Bransfield Strait. *Antarctic Sci.* 5:335-338.
- CASAUX, R., E. BARRERA-ORO, M. FAVERO, AND P. SILVA. 1995a. New correction factors for the quantification of fish represented in pellets of the Blue-eyed Shag *Phalacrocorax atriceps*. *Comm. Conserv. Antarctic Mar. Living Resour. Ecosys. Monitoring Manage. Working Group, Document 95/83:1-18*, Siena, Italy.
- CASAUX, R., M. FAVERO, E. BARRERA-ORO, AND P. SILVA. 1995b. Feeding trial on an Imperial Cormorant *Phalacrocorax atriceps*: preliminary results on fish intake and otolith digestion. *Marine Ornithol.* 23:76-82.
- CASAUX, R., A. MAZZOTTA, AND E. BARRERA-ORO. 1990. Seasonal aspects of the biology and diet of nearshore Nototheniid fish at Potter Cove, South Shetland Islands, Antarctica. *Polar Biol.* 11:63-72.
- CLARKE, J., K. KERRY, AND E. FRANCHI. 1995. Differences in the foraging strategies of male and female Adelie Penguins. *Comm. Conserv. Antarctic Mar. Living Resour. Ecosys. Monitoring Manage. Working Group, Document 95/46*, Siena, Italy.
- COOPER, J. 1985a. A note on the diet of Cape Cormorant *Phalacrocorax capensis* at Mercury Island, South West Africa, in November 1978. *S. Afr. Mar. Sci.* 3:129-130.
- COOPER, J. 1985b. Biology of the Bank Cormorant, part 3: foraging behaviour. *Ostrich* 56:86-95.
- COOPER, J. 1986. Diving patterns of cormorants (Phalacrocoracidae). *Ibis* 128:562-569.
- CORIA, N., R. CASAUX, M. FAVERO, AND P. SILVA. 1995. Analysis of the stomach content in the Blue-eyed Shag *Phalacrocorax atriceps bransfieldensis*, at Nelson Island, South Shetland Islands. *Polar Biol.* 15:349-352.
- CROXALL, J. P., AND G. S. LISHMAN. 1987. The food and feeding ecology of penguins, p. 101-133. *In* J. P. Croxall [ed.], *Seabirds, feeding ecology and role in marine ecosystems*. Cambridge Univ. Press, Cambridge.
- CROXALL, J. P., Y. NAITO, A. KATO, P. ROTHERY, AND D. BRIGGS. 1991. Diving patterns and performance in the Antarctic Blue-eyed Shag *Phalacrocorax atriceps*. *J. Zool.* 225:177-199.
- CROXALL, J. P., P. A. PRINCE, AND C. RICKETTS. 1985. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea, p. 516-533. *In* W. R. Siegfried, P. R. Condy, and R. M. Laws [eds.], *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin.
- DEL HOYO, J., A. ELLIOT, AND J. SARGATAL. 1992. *Handbook of the birds of the world*. Vol. 1. Lynx Edicions, Barcelona.
- DUFFY, D. C., AND S. JACKSON. 1986. Diet studies of seabirds: a review of methods. *Colonial Waterbirds* 9:1-17.
- GREEN, K., R. WILLIAMS, AND D. SLIP. 1990a. Diet of the Macquarie Island Cormorant *Phalacrocorax atriceps purpurascens*. *Corella* 14:53-55.
- Green, K., R. Williams, E. Woehler, H. Burton, N. Gales, and R. Jones. 1990b. Diet of the Heard Island Cormorant *Phalacrocorax atriceps nivalis*. *Antarctic Sci.* 2:139-141.
- HECHT, T. 1987. A guide to the otoliths of Southern Ocean fishes. *S. Afr. J. Antarct. Res.* 17:1-87.
- KATO, A., J. P. CROXALL, Y. WATANUKI, AND Y. NAITO. 1991. Diving patterns and performance in male and female Blue-eyed Cormorants *Phalacrocorax atriceps* at South Georgia. *Marine Ornithol.* 19:117-129.
- KATO, A., I. NISHIUMI, AND Y. NAITO. 1995. Sexual differences in the diet of King Cormorants at Macquarie Island. *Polar Biol.* 16:75-77.
- MARCHANT, S., AND P. H. HIGGINS. 1990. *Handbook of Australian, New Zealand and Antarctic birds*. Vol. 1. Oxford Univ. Press, Melbourne.
- SHAW, P. 1984. Factors affecting the breeding performance of the Antarctic Blue-eyed Shag (*Phalacrocorax atriceps*). *Polar Biol.* 11:63-72.

- crocorax atriceps bransfieldensis*). Ph.D. diss., Univ. Durham, England.
- VELDKAMP, R. 1995. Diet of cormorants *Phalacrocorax carbo sinensis* at Wanneperveen, The Netherlands, with special reference to bream *Abramis brama*. *Ardea* 83:143–155.
- VOLKMAN, N. J., P. PRESLER, AND W. TRIVELPIECE. 1980. Diets of Pygoscelid penguins at King George Island, Antarctica. *Condor* 82:373–378.
- WANLESS, S., M. HARRIS, AND J. MORRIS. 1995. Factors affecting daily activity budgets of South Georgian Shags during chick rearing at Bird Island, South Georgia. *Condor* 97:550–558.
- WANLESS, S., M. HARRIS, AND F. RUSSELL. 1993. Factors influencing food-load sizes brought in by shags *Phalacrocorax aristotelis* during chick rearing. *Ibis* 135:19–24.
- WIENS, J. A. 1984. Modeling the energy requirements of seabird populations, p. 255–284. In G. C. Whitow and H. Rahn [eds.], *Seabird energetics*. Plenum Press, New York.
- ZIJLSTRA, M., AND M. R. VAN EERDEN. 1995. Pellet production and use of otoliths in determining the diet of cormorants *Phalacrocorax carbo*: trials with captive birds. *Ardea* 83:123–130.