Antarctic Science 19 (1), 55–63 (2007) © Antarctic Science Ltd Printed in the UK DOI: 10.1017/S0954102007000089

Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour

TIMOTHÉE R. COOK[1]*, YVES CHEREL[1], CHARLES-ANDRÉ BOST[1] and YANN TREMBLAY[2]

[1]*Centre d'Etudes Biologiques de Chizé, CEBC - CNRS UPR 1934, Villiers-en-bois, F-79360 Beauvoir-sur-Niort, France*
[2]*University of California Santa Cruz, Long Marine Laboratory. 100 Shaffer Road, Santa Cruz, CA 95060, USA*
**cook@cebc.cnrs.fr*

Abstract: We compared, for the first time the foraging ecology of both sexes of the blue-eyed Crozet shag (*Phalacrocorax melanogenis*), using ventrally attached time depth recorders to investigate differences in time-budget and diving behaviour between the sexes during the chick-rearing. Males were the only ones to dive over 55 m. Females dived mostly between 15 and 35 m, a zone poorly used by males. Females foraged mostly in the morning and males in the afternoon. Females also spent one hour longer diving per day compared to males. There were differences in diving strategies and diet, indicating that both sexes targeted essentially the same prey, but of different sizes, males specializing in bigger fish. Although the relationship between sexual dimorphism and diving depth was positive (larger animals diving deeper), evidence suggests that body size (in terms of oxygen storage capacity) is not sufficient to explain so many differences in foraging ecology. Instead, we propose prey size (possibly driven by a limitation of prey handling ability in relation to beak size) could be an essential factor in shaping the male/female behavioural segregation in the Crozet shag; future studies should concentrate on this particular aspect.

Received 12 June 2006, accepted 12 September 2006

Key words: blue-eyed shags, diving behaviour, ecological selection, niche divergence, sexual dimorphism, time-budget

Introduction

Seabirds present an opportunity to assess sexual dimorphism in the light of multiple factors. For example, most seabirds display sexual size dimorphisms (Fairbairn & Shine 1993) and may show sexual differences in foraging ecology (Weimerskirch *et al.* 1993). Recently, studies have tried to understand the evolutionary forces responsible for sexual differences in seabirds, be these morphological, physiological, or behavioural (González-Solís *et al.* 2000, Shaffer *et al.* 2001, Jones *et al.* 2002, Lewis *et al.* 2002, Lormée *et al.* 2003). Insights have been gained in the study of systems with larger males and sex-specific foraging strategies. For example, clearly separate foraging zones between the sexes are thought to be derived from a situation of competition for food (González-Solís *et al.* 2000, Shaffer *et al.* 2001). Such hypotheses remain nevertheless difficult to demonstrate because behaviours may be the result of past competition, or because interactions between individuals at sea are generally unseen.

Blue-eyed shags are benthic foot-propelled divers which have an important role in the Southern Ocean's marine food web as they are among the main top predators, with gentoo penguins, of coastal benthic fish (Casaux & Barrera-Oro 2006). The blue-eyed shag complex represents a group of 13 species of closely related cormorants living in the Southern Ocean, each defined by its geographical location (Orta 1992). The four species living respectively on the Antarctic Peninsula, at South Georgia, and on Macquarie and Heard islands, exhibit certain sexual differences in foraging ecology, particularly with respect to activity patterns, diving depth, and prey size (Bernstein & Maxson 1984, Croxall *et al.* 1991, Kato *et al.* 1996, Green & Williams 1997). In some cases, males have been found to dive deeper than females. Some authors have suggested that differences in diving depth and prey size may be an adaptation to reduce food competition between the sexes, and that deeper dives by males may be possible because of their greater body mass (Kato *et al.* 1999).

In this context, we investigated the foraging ecology of the Crozet shag (*Phalacrocorax melanogenis*, Blyth 1860), a species of sexually dimorphic blue-eyed shag (males 20% heavier than females, Derenne *et al.* 1976) for which no study on sex-based differences in foraging behaviour had yet been undertaken. In a previous study testing the use of the ventral attachment technique of Time-Depth-Recorders (Tremblay *et al.* 2003) in Crozet shags (Tremblay *et al.* 2005), we described for the first time the time-budget and diving behaviour of this species. We showed that these birds were "hard workers" during the chick rearing period, spending approximately six hours per day foraging in cold sea water and diving to great depths (maximum 145 m) to catch benthic nototheniid fish.

In the present study, we wanted to verify if sex-specific foraging behaviour exists in this species, and if so, to discuss its possible relationship with sexual dimorphism. Our objectives were thus to compare the detailed behaviour

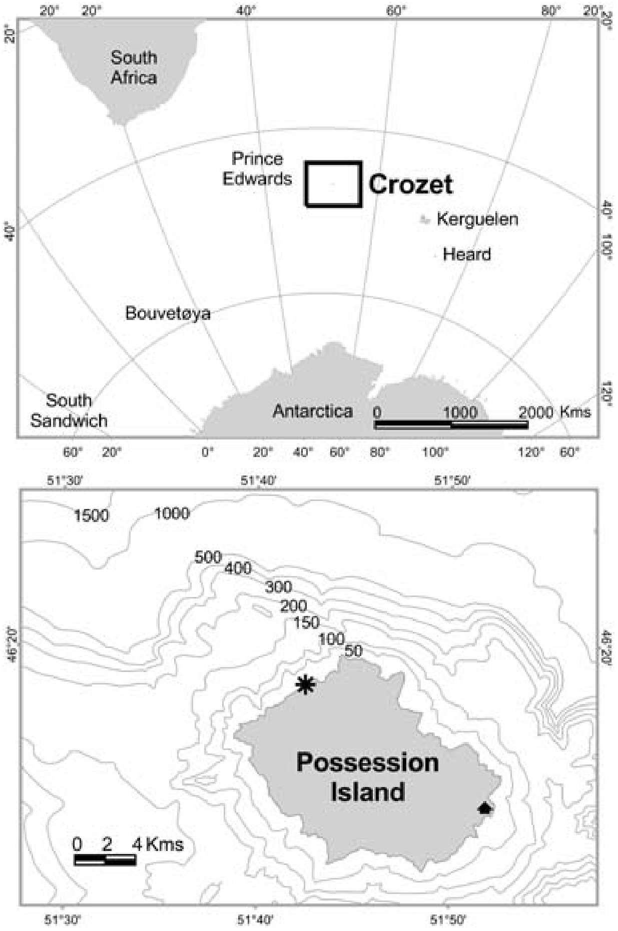

Fig. 1a. General location of the Iles Crozet in the Southern Ocean. **b.** Map of Possession Island. The Alfred Faure station is located on the south-east of the island (black shed). The study colony is on the north-west side of the island (black asterisk).

of male and female Crozet shags during chick rearing: are there any sexual differences in foraging ecology when looking closely at certain foraging parameters? For example, differences in daily time spent at sea can reflect different foraging efficiencies or strategies. We therefore investigated to see if there were any sex-based differences in time-budget, in activity patterns, and in flight duration. Differences in dive depth can be related to a number of hypotheses, such as differences in oxygen reserves or prey choice. We thus also tested for sex-based differences in diving behaviour. Our results were compared to existing data in the literature, and the different hypotheses as to the evolutionary processes relating dimorphism to behaviour were reviewed.

Material and methods

Study site, birds and general procedure

Field work was conducted at Iles Crozet (Southern Ocean), on Ile de la Possession, a small island of volcanic origin with very little continental shelf, and deep surrounding waters (Fig. 1). The study took place between 28 January and 9 February 1999 at Pointe Basse (46°21'S, 51°42'E; Local Time = UTC + 3:20) in a small colony of Crozet shags (13 nests).

Six males and six females from six pairs of Crozet blue-eyed shags were studied during the middle to late chick-rearing period, when partners increment (sometimes overlapping) the number of foraging trips (reducing the duration of the trips), usually alternating the time at sea, with females leaving for the first time early in the morning, and males later on (personal observation, Cook *et al.* 2006). There were 1.8 ± 0.7 chicks per nest (1–3). Mean chick mass was 1807 ± 574 g (675–2435 g), mean cumulative mass per nest 3313 ± 1181 g (675–6475 g), and age of chicks between 10 and 50 days. The birds were captured at night by hand, and weighed (precision ± 25 g) using a spring balance, measured for sexing, and a Time-Depth Recorder (TDR MK7 Wildlife Computers, Woodinville, WA, USA) was attached ventrally according to Tremblay *et al.* (2003) for a 4–5 day period, using cyanoacrylate glue (Loctite 401) and plastic ties (total initial handling time ≈ 5 min). Loggers were retrieved immediately after birds came back from the sea. Food samples were then taken. The stomach contents were sampled (one food sample per individual). Contents were retrieved with birds regurgitating spontaneously when handled: this technique brings mainly qualitative data about the food load (prey species and sizes). Four contents were not retrieved because the birds would not regurgitate, and one bird was apparently empty. Another content from a non study male was also collected. A total of eight stomach contents were thus frozen for later analysis at the laboratory (from three females and five males). Fish species were determined according to Gon & Heemstra (1999), using the whole fish, when it was preserved, or the otoliths. Otoliths were measured with a precision of ± 0.1 mm. For the regressions relating otolith length to standard length of fish see Tremblay *et al.* (2005). Prey size differences between sexes were compared using mean standard length of total fish items per individual content.

This study was approved by the ethics committee of the French Polar Institute (Institut Paul Emile Victor–IPEV). All animals in this study were cared for in accordance with its guidelines.

Data analysis

Time budget analysis was performed using the advantages inherent in the ventral attachment technique (Tremblay *et al.* 2003). Daily diurnal time budgets were calculated for civil day time (time bounded by the two moments when the Sun is 6° under the horizon). Foraging trips and flights were determined by simultaneous reading of depth, light, and temperature profiles in relation to time. The mean radius of the foraging area was estimated with flight durations using a flight speed of $V = 14.7 + 0.154W$ m.s^{-1} (cormorant subjected to across winds), where W is wind speed (Spear & Ainley 1997). Average wind speed was 10 m.s^{-1} from a west or north-westerly direction (1999 data from Topex-Poséidon satellite at website http://www-aviso.cls.fr). Cormorant flight speed was therefore estimated as 16.2 m.s^{-1}, and birds were assumed to fly from one point to another in a straight line, and never to cut across land (personal observations and Orta 1992). Dive parameters were gathered using our own software for dive analysis (Tremblay & Logette unpublished).

Dive duration, post dive interval (PDI), bottom time (defined as the time spent in the zone ≥ 80% of maximum depth; Kato *et al.* 1999), descent and ascent rates (ratio between the depths where the bottom time begins or ends and the time it takes to commute between that depth and the surface), dive efficiency (bottom time/[dive duration + post dive interval]), and the behavioural Aerobic Dive Limit (bADL), were calculated. The bADL is the breath-hold duration after which metabolism is anaerobic oriented, estimated from behaviour. The method used is the graphic method by Kooyman & Kooyman (1995). The bADL was estimated as the inflection of the scattergram (PDI = f[dive duration]): the contour of the minimum PDI values (the most relevant physiologically) are a result of increased blood lactate. As increased blood lactate during the dive has the consequence of increasing massively PDIs, the relation between PDI and dive duration for dives > to bADL becomes exponential (for the scattergram at Crozet, see Tremblay *et al.* 2005).

Other less commonly used dive parameters were also calculated to compare different underwater hunting strategies between the sexes during the bottom phase, such as the number of bottom wiggles (number of vertical direction changes), the depth activity index (vertical distance travelled per second of bottom phase), and the number of light wiggles at the bottom (number of light variations). These parameters have proven useful in describing at sea behaviour of benthic divers (Tremblay & Cherel 2000). As it has been shown that Crozet shags are essentially benthic divers (Tremblay *et al.* 2005), we also calculated intra depth zone (IDZ) indexes for the dives to assess whether a sex was more or less benthic than the other. The IDZ index shows the percentage with which an animal tends to dive serially to a similar depth (Tremblay & Cherel 2000). If the maximum depth of a dive was ± 10% of the maximum depth of the preceding dive, it was considered as an intra depth zone dive.

Statistics

Comparison between sexes of time-budget and daily foraging parameters was done using days with complete daily cormorant behaviour recording (27 for males, 28 for females), corresponding to a total 4558 dives in females and 3212 dives in males. Comparison of dive parameters was performed on the total of dives recorded over the study period, counting days with complete recording of behaviour and days with data recorded over only part of the day (4890 dives in females and 3300 dives in males).

In order to avoid problems of pseudo-replication and individuals with varying statistical weights, we compared sexes using generalized linear mixed-effects models (GLMM, Schall 1991) fitted by restricted maximum likelihood (REML, Patterson & Thompson 1971). In all cases, we set sex as a fix factor and bird identity as a random factor. There was no relation per nest between the daily time spent at sea in one partner compared to the other (Wilcoxon test for paired samples: $Z = 1.15$, $P = 0.251$). Nevertheless, we nested the bird identity and nest number when comparing time-budget, daily foraging parameters, and flight durations for commuting from the colony to the sea surface and back (for a total of 123 foraging trips for females and 137 foraging trips for males). In order to compare the dive parameters between the sexes for any given depth (independently from depth), dive depth was set as a covariate. Dive parameters were log-transformed to adjust for skewed distributions.

Eventually, we used the Kolmogorov-Smirnov test to compare frequency distributions of dives, the Spearman's rank-order correlation to relate body mass to diving depth, and the Mann-Whitney *U*-test for independent samples when comparing body measurements and diet samples.

Data were analysed statistically using R 2.3.1 (Ihaka & Gentelman 1996), Statistica 6.1 and Sigmaplot 8.0, with an α-level of significance of $P < 0.05$. The mean values are given ± SD. Finally, maps were constructed using Arcview 3.2.

Results

Activity patterns, time budget, and foraging areas

Females tended to forage before midday, while males

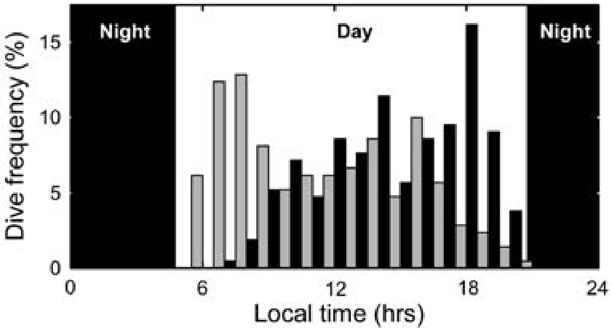

Fig. 2. Dive frequency of female (grey) and male (black) Crozet shags in relation to time of day. Day and night are defined in relation to the civil day (Sun zenith at 12:05).

Table I. Foraging and time budget parameters in male and female Crozet shags. Time-budget is presented per day for the period of daylight (15 h 50 min, see Materials and methods).

Parameter	Females	Males	df	*t*	*P*
Time at colony	09:33 ± 01:15	10:30 ± 01:05	5	1.45	0.204
Time at sea	06:27 ± 01:15	05:30 ± 01:05	5	-1.45	0.204
Flying	00:25 ± 00:06	00:21 ± 00:06	5	-1.13	0.308
Diving	03:10 ± 00:45	02:07 ± 00:25	5	-3.07	0.027
On water	02:52 ± 00:33	03:01 ± 00:46	5	0.38	0.718
Trip duration	01:26 ± 00:14	01:25 ± 00:33	5	-0.24	0.810
Trips / day	4.5 ± 0.8	4.2 ± 1.1	5	-0.64	0.550
Diving bouts / day	11.6 ± 2.8	10.1 ± 2.9	5	-0.79	0.460
Dives / day	166 ± 70	115 ± 85	5	-1.86	0.120
Diving bouts / trip	2.6 ± 0.4	2.5 ± 0.8	5	-0.01	0.987
Dives / trip	37 ± 14	25 ± 14	5	-1.25	0.239
Dives / bout	15 ± 8	12 ± 10	5	-0.59	0.567

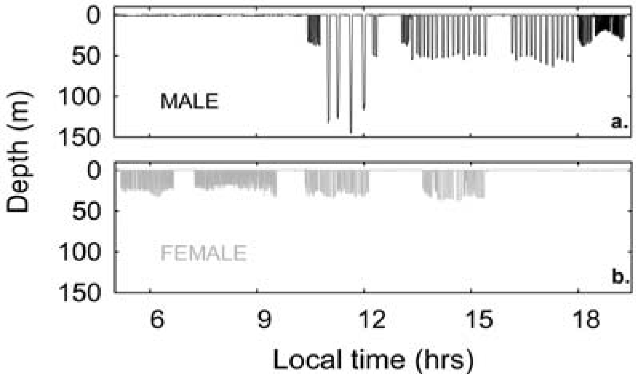

Fig. 3a. Complete daily dive sequence recordings for a male Crozet shag; this male performed very deep dives this day (max. 145 m). **b.** Dive sequence recording on the same day for a female, partner of the above mentioned male.

tended to forage in the afternoon (Kolmogorov-Smirnov test: $D = 0.36$, $P < 0.001$). Indeed, 67% of female trips (60% of female dives) were carried out before 12:05 (the Sun's zenith time), and 68% of male trips (75% of male dives) took place afterwards (Fig. 2).

No significant differences were found between the sexes in foraging parameters (for a list of parameters, see Table I), except in time-budget. Females spent daily one hour longer under water (diving) compared to males, with males diving for only 67% of total female diving time. The comparison between sexes of foraging parameters is summarized in Table I.

Flights out to sea (leaving the colony and entering the water for the first time) and flights back to the colony (leaving the sea surface and landing at the colony) were compared between sexes. Outbound flight time lasted 63 ± 43 sec (7–192 sec) for males and 97 ± 81 sec (9–424 sec) for females ($t = -1.30$, $P = 0.044$). Inbound flight time lasted 97 ± 47 sec (13–266 sec) for males and 114 ± 86 sec (16–687 sec) for females ($t = -0.22$, $P = 0.359$). Mean radius of foraging area was calculated as 1710 m in females and 1300 m in males (using duration of inbound flights). Finally, the relation between mean daily outbound flight durations (moving out from the colony to the sea surface) and maximum individual daily dive depth was strong in males ($y = 0.37x + 40.94$, $r^2 = 0.30$, $P = 0.019$) and absent in females ($y = 0.88x + 59.93$, $r^2 = 0.08$, $P = 0.149$).

Table II. Mean morphometric and dive parameters for male and female Crozet shags. Maximum for each sex is the mean of all individual maximum values.

Parameter	Females	Males	U	*P*
Body mass (g)	2112 ± 109	2542 ± 133	0	< 0.01
Culmen length (mm)	56 ± 2	61 ± 1	0	< 0.01
Wing length (mm)	278 ± 5	291 ± 9	4.5	0.029
Tarsus length (mm)	66 ± 1	69 ± 1	0	< 0.01
Maximum dive depth (m)	34 ± 13	93 ± 44	2	0.011
Mean dive depth (m)	20 ± 13	36 ± 35	17762	< 0.001
Maximum dive duration (s)	158 ± 49	280 ± 78	5	0.032
Mean dive duration (s)	84 ± 53	124 ± 104	10463	< 0.0001

Body size, dive depth and dive duration

Body mass and body size of males were greater than those of females. Males were 20% heavier and 4–9% larger for three structural characteristics compared to females (Table II). In all birds, absolute maximum depth reached per individual was positively related to body mass (Spearman's rank-order correlation: $r_s = 0.77$, $P < 0.01$; Table II). Finally, we calculated the theoretical maximum dive depth and dive duration for males and females using our birds' body masses and a regression from the literature based on data from 13 different species of cormorants, and linking body mass to dive performance (Schreer & Kovacs 1997). The difference predicted by this model between mean values per sex was 13 m in maximum dive depth, and 11 s in maximum dive duration. Our collected data show a difference of 59 m

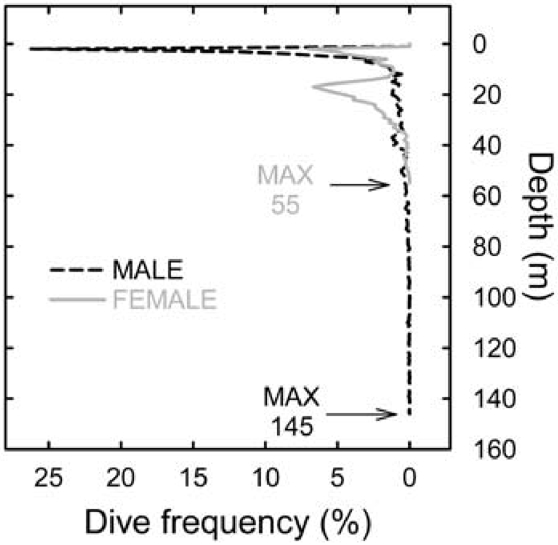

Fig. 4. Diving depth frequency for male and female Crozet shags.

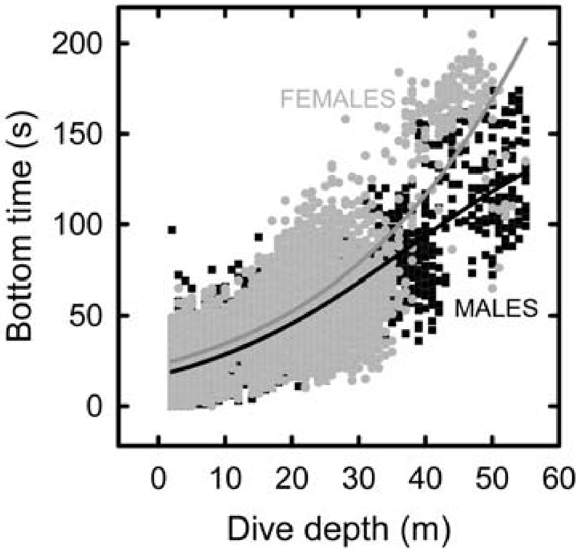

Fig. 5. Relation between dive depth and bottom time for male and female Crozet shags for dives between 0 and 55 m (maximum female dive depth). Female dives are represented by grey circles ($r^2 = 0.60$, $n = 4890$, $P < 0.0001$), and male dives by black squares ($r^2 = 0.76$, $n = 3092$, $P < 0.0001$).

in maximum dive depth, and 122 s in maximum dive duration.

Diving behaviour

Maximum dive depth was 145 m for males (Fig. 3) and 55 m for females. Frequency distributions of dive depth, dive duration, post dive interval, and bottom time were different between the sexes (Kolmogorov-Smirnov test: all $D > 0.06$, all $P < 0.001$). Although males carried out dives to the greatest depths (50–145 m), most of their dives were in the shallowest depths, 52% of dives being < 5 m. Females used shallow waters to a lesser extent, and foraged more intensively in the 15–35 m zone (Fig. 4).

Female dives averaged a maximum depth of 20 ± 13 m, lasted 84 ± 53 sec (2–250 sec), with a post dive interval of 78 ± 83 sec (0–800 sec), and a bottom time of 62 ± 44 sec (0–225 sec). Male dives averaged a maximum depth of 36 ± 35 m, lasted 124 ± 104 sec (2–371 sec), with a post dive interval of 163 ± 183 sec (0–800 sec), and a bottom time of 83 ± 76 sec (0–241 sec). Behavioural ADL was estimated at ≈ 240 sec for both males and females. The percentage of dives ≥ bADL in duration was 20% for males and < 1% for females. For both sexes, all dives ≥ bADL were ≥ 47 m in maximum depth.

Table III. Comparison between sexes of detailed dive parameters independently from dive depth.

Parameter	df	*t*	*P*
Descent rate (m.s^{-1})	10	2.90	0.015
Bottom time (s)	10	-3.21	0.009
Ascent rate (m.s^{-1})	10	0.45	0.662
Dive duration (s)	10	-3.58	0.005
PDI (s)	10	-1.60	0.139
Dive cycle time (s)	10	-2.77	0.019
Dive duration / PDI	10	-0.87	0.401
Efficiency	10	-0.84	0.416
Bottom wiggles	10	-2.51	0.030
Depth activity index (m)	10	-1.31	0.219
Light wiggles	10	-3.17	0.009
IDZ (%)	10	-1.30	0.221

Detailed dive parameters were compared between the sexes independently from dive depth (Table III). At same dive depth, females carried out longer dives with longer bottom times. These differences increased with maximum dive depth (Fig. 5). Also, females carried out a greater number of bottom wiggles and light wiggles. IDZ values (60.3 ± 14.8% in females and 55.6 ± 8.4% in males) were also not significantly different between sexes. Using mean values of dive parameters for dives in the 35–55 m zone, a model of the female and male dive cycle was constructed to illustrate the differences (Fig. 6).

Diet

Diet sample size was unfortunately reduced. The contents retrieved from the eight birds contained exclusively the nototheniid fish *Paranotothenia magellanica* (occurrence: 87.5% of total number of samples), except for one male sample, which contained also one item of the nototheniid

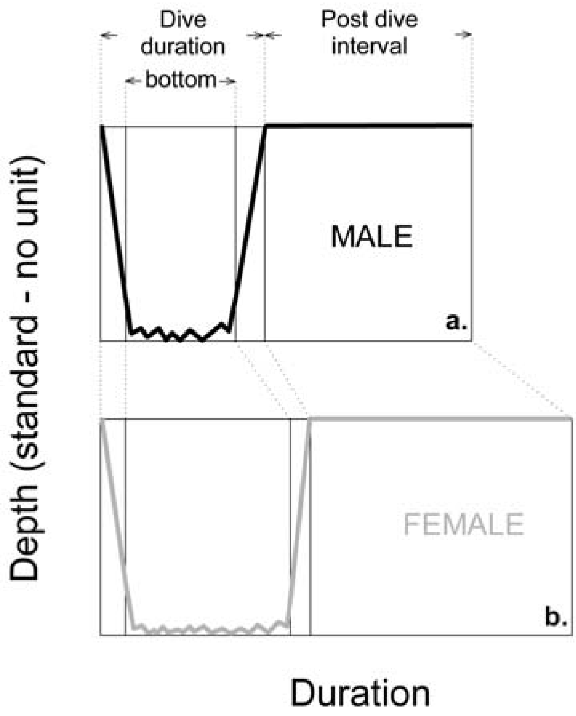

Fig. 6a. Average dive cycle for dives carried out by males between 35–55 m. **b.** Average dive cycle for dives carried out by females in the same depth zone.

fish *Notothenia coriiceps*, and another male, which contained only the nototheniid fish *Gobionotothen marionensis*. Mean total fresh mass of contents was 171 ± 44 g for females and 134 ± 58 g for males. There was a difference in estimated standard length of fish caught by females (34 ± 4 mm, range: 12–126 mm) and males (105 ± 29 mm, range: 8–176 mm) (Mann-Whitney U-test: $U = 0$, $n = 8$, $P = 0.025$).

Discussion

Like several other species of blue-eyed shags, the Crozet shag exhibited important sex-based differences in foraging ecology (Table IV). The two sex-specific behaviours described here could represent two different hunting strategies for the exploitation of two separate niches. These were based on a temporal and maybe spatial segregation in foraging activity, on differences in dive depths and dive parameters, and possibly on a segregation at the dietary level.

Spatial and temporal segregation

The vertical distribution of the foraging areas used by males and females showed considerable differences. Males were the only sex to forage over 55 m deep, yet they foraged mostly in very shallow waters (Fig. 4). As dives were essentially benthic, this vertical difference in foraging area has to be associated with a horizontal segregation. This was confirmed by the positive relation between daily flight duration moving out from the colony to the sea surface and maximum daily dive depth in males. This relation was absent in females. Females thus exhibited a pattern consistent with the exploitation of the 15–35 m (Fig. 4) shallow water band just off the coastline (an "along isobaths" pattern of movement). Males also displayed this pattern, but, occasionally reaching deeper zones, they also displayed a straight pattern of movements between the very shallow coastal waters and the more offshore deeper zones (an "across isobaths" pattern of movement).

The potential overlap in foraging depths/zones between males and females was reduced by the temporal segregation, females foraging more in the morning and males more in the afternoon. Casaux *et al.* (1990) observed that some fish species eaten by the Antarctic blue-eyed shag were more active in the afternoon, precisely when the male cormorants were at sea, suggesting that male/female spatial and temporal segregation might be driven by a difference in targeted preys. Further investigation is therefore required to properly assess the relation between activity patterns and prey choice.

Table IV. References of articles (with study site and species) where authors found characteristics in the foraging behaviour of a blue eyed-shag similar to one described in the present study.

Parameter	Reference
Males dived deeper	8, 10, 11
bADL was exceeded	4, 5, 7
At same max. depth, bottom time of females was greater	11
Fish captured by males were bigger	2, 3, 9, 10, 11
Females started foraging before males in the daytime	1, 2, 6, 8, 10, 11

Antarctic Peninsula, South Shetland Islands: *Phalacrocorax bransfieldensis*.
1. Bernstein & Maxson 1984, 2. Favero *et al*. 1998, 3. Casaux *et al*. 2001.
South Georgia: *P. georgianus*. 4. Croxall *et al.* 1991, 5. Wanless *et al.* 1992, 6. Wanless *et al.* 1995, 7. Bevan *et al.* 1997.

Heard Island: *P. nivalis*. 8. Green & Williams 1997.
Macquarie Island: *P. purpurascens*. 9. Kato *et al.* 1996, 10. Kato *et al.* 1999, 11. Kato *et al.* 2000.

Two hunting strategies?

In males, 80% of dives > 55 m (20% of all dives) exceeded the bADL. In females, on the other hand, only < 1% of all dives exceeded the bADL. Diving > 55 m thus potentially required anaerobic metabolism. These deep/long male dives had low dive efficiencies (Tremblay *et al.* 2005), so that a relatively short time was spent at the bottom. Males thus had to push their physiological limits more than females. Burger (1991) hypothesized that anaerobic metabolism could be a way of extending bottom time, particularly in the case of deep dives. In our case, anaerobic metabolism could mostly be used to access deeper feeding grounds (males). As females did not seem to resort to anaerobic metabolism, this pathway was not used to spend more time at shallow depths. This is turn suggests that deep feeding zones used by males may be associated with a relatively high probability of encountering prey, since little time can be spent searching while at the bottom. Favero *et al.* (1998) suggested deep dives could yield bigger fish for Antarctic shags. Our only diet from deep dive foraging did not support this hypothesis and shows that small fish can be caught at deep depths by males. Although males dived deeper, it is important to note that this was done only occasionally, and that they generally dived to shallow depths.

Females dived efficiently compared to the very deep or very shallow male dives in terms of breathing optimality, as they dived mostly between 15–35 m (Fig. 4), a depth zone for which dive durations fit with the highest dive duration/PDI ratio in this species (Tremblay *et al.* 2005), reinforcing the idea of an aerobic oriented strategy. For dives of similar depth, there was no real difference in the percentage of IDZ dives between the sexes, suggesting they targeted prey with the same ecology (benthic and epibenthic fishes; Ishikawa & Watanuki 2002). The male dives had shorter bottom times (Fig. 5) and had fewer vertical zigzags (depth wiggles) or light wiggles than female dives (Table III, Fig. 6). This could be related to different prey types targeted by each sex. In addition to spending less time at the bottom of the dives, males also spent less time per day diving (Table I). This probably corresponded to a greater global daily time spent at sea in females, though it was not significant. Male diving strategy could be consistent with feeding on bigger prey, and this needs to be confirmed by further diet data. Given their mass (and associated size) *Paranotothenia magellanica* individuals caught by males and females were most probably juveniles from different cohorts (Miller 1993, White 1998).

To conclude, the vertical and temporal segregation observed above might be associated with different hunting strategies that could be consistent with different prey size targeted by males and females respectively.

Dive depth and body size

Is shallower diving by females a consequence of smaller body size? For diving air breathing animals, there is a positive allometric relationship between diving capacity (duration and depth) and body mass (Schreer & Kovacs 1997). A greater body mass confers a greater oxygen reserve, for a proportionally lower mass-specific energy expenditure. Body mass difference between male and female cormorants has been an argument for explaining superior male diving performances in Japanese cormorants *Phalacrocorax capillatus* (Watanuki *et al.* 1996) and *P. filamentosus* (Kato *et al.* 1998, 1999) and in the Macquarie blue-eyed shag *P. purpurascens* (Kato *et al.* 1999). Here, mean male body mass was 20% larger than mean female body mass and the relationship between body mass and absolute maximum depth reached per individual was positive. Yet, in this study, the male individual which dived the deepest was also the lightest of all males (2350 g) and exceeded the heaviest female by only 50 g. In addition, bADL was the same for males and females. Finally, when using the regression calculated by Schreer & Kovacs (1997) and linking body mass to maximum dive duration and depth, we found that our birds did not fit at all with the model.

Maximum dive depth/duration could therefore more likely be related to sex than to body mass. Similar maximum dive durations were reported in male and female blue-eyed shags (Kato *et al.* 2000), even though males dived deeper. In the South-Georgia blue-eyed shag *P. georgianus*, maximum recorded dive depth for females had been 63 m (Kato *et al.* 1992) until nine years later another study reported in the Antarctic blue-eyed shag *P. bransfieldensis* a maximum depth of 113 m (Casaux *et al.* 2001). In the latter study, females dived on average deeper than the males during two consecutive years, but males still captured bigger and/or different specimens of fish than did the females.

Consequently, and as is consistent with the two sexually distinct hunting strategies described in this study, male and female differences in diving behaviours could represent an adaptation to distinct targeted prey size, rather than be a consequence of different size-related diving capacities (oxygen storage ability).

Conclusions

The limited number of study birds requires cautious extrapolation. In particular, the diet sample was unfortunately reduced, indicating rather a trend than a settled difference. Also, the use of flight durations gives only an approximation of foraging range, but does not locate foraging grounds precisely. Nevertheless, birds were followed over 4–5 days, a period long enough to compensate somewhat for the number of individuals, suggesting the findings here are to be considered seriously. More importantly, many of the sex-based differences observed appear to match with some observed in other species of blue-eyed shags (Table IV), flagging the Crozet shag as another cormorant from the blue-eyed shag complex to display sex-specific foraging behaviour.

The reasons for splitting niches remain unclear. Future studies should obviously concentrate on differences in prey species, and particularly in prey size. Do female blue-eyed shags actually always catch smaller fish than males? If so, what does this mean? Does body size influence the size range of the fish which can be caught? Niche characteristics can be determined by characteristics of sexual dimorphism, such as culmen length and/or bill depth (Selander 1966). Bill depth is the most discriminating morphometric parameter for sexing great cormorants *Phalacrocorax carbo* (Koffijberg & Van Eerden 1995) and blue-eyed shags (Malacalza & Hall 1988), and it has been shown, as for bill width, to also be important in determining handling and snapping power in birds (Boag & Grant 1981, Smith 1987). Showing females are unable to catch the bigger fish because their handling power is smaller than males' - because their beaks are smaller than males' - requires an experimental approach. Favero *et al.* (1998) proposed that the niche splitting could maximize the chances of one member of the pair locating food for the chicks, thus increasing the efficiency of the pair. This would agree with the possible two hunting strategies described here. These authors equally suggested this could reduce intra-specific competition but this would be more difficult to understand if the two sexes feed on the same fish species.

It is not at all obvious that all of the sex-specific behaviours observed in the blue-eyed shag are related to niche splitting strategies. Even though Casaux *et al.* (2001) proposed that the sex-specific foraging activity rhythms could be related to the schedule of prey activity, this remains to be demonstrated. It is possible sex-specific rhythms could depend on pressures encountered not at sea, but on land. For example, it may be that males forage mainly during the second part of the day because they bring back bigger food loads, and this provides a greater survival probability for chicks as they have to fast during the night and during a large part of the following morning until the females return with more food. Indeed, male Crozet shags were more efficient than females, targeting bigger prey in shallow waters closer to the colony, and spending less time daily in doing so, as they spent only 67% of the time underwater compared to females. In the future, exploring the energetics of the Crozet shag (measuring precisely costs and benefits of foraging behaviour in relation to time budget) will be necessary in order to understand the reasons why the males are so efficient.

The exploitation of two niches by both sexes of the Crozet shag using different strategies concurs with some behavioural sexual differences observed for four other blue-eyed shags, and tends to reinforce the proposition of uniformity in the blue-eyed shag complex at a behavioural level (Table IV, though females may occasionally dive deeper than males, Casaux *et al.* 2001). Sex specific behaviour in the blue-eyed shag species could thus have a strong genetic background. The relative contribution of sexual selection in the shaping of sexual dimorphism in blue-eyed shags is important when studying the relation between sexual dimorphism and sexual foraging behaviour. Male blue-eyed shags may fight ferociously when competing for females or nest positions (personal observation). It is taken for granted that sexual dimorphism in the cormorant family is related to sexual selection, yet this has rarely been measured (Childress & Bennun 2002). In conclusion, blue-eyed shags display sexual differences, and yet the reasons for some traits remain enigmatic. This group still appears as a relevant model for studying the origins and evolution of sex-specific foraging behaviour.

Acknowledgements

The authors would like to thank T. Guionnet, J. Martin, S. Shaffer and A. Hoecker for their help in the field. The authors also thank from the Centre d'Etudes Biologiques de Chizé (CEBC), C. Trouvé, for her help on stomach content analysis, X. Bonnet, for his exciting explanations on sexual dimorphism and ecological selection, and L. Hardouin, for his guidance into the realm of R and generalized linear mixed-effects models. We also thank two anonymous reviewers for their pertinent remarks on the manuscript. This work was supported financially and logistically by the Institut Paul Emile Victor (IPEV, Program 109) and the Terres Australes et Antarctiques Françaises (TAAF).

References

Bernstein, N.P. & Maxson, S.J. 1984. Sexually distinct daily activity patterns of blue-eyed shags in Antarctica. *Condor*, **86**, 151–156.

Bevan, R.M., Boyd, I.L., Butler, P.J., Reid, K., Woakes, A.J. & Croxall, J.P. 1997. Heart rates and abdominal temperatures of free-ranging South Georgian shags, *Phalacrocorax georgianus*. *Journal of Experimental Biology*, **200**, 661–675.

Boag, P.T. & Grant, P.R. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. *Science*, **214**, 82–85.

Burger, A.E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. *In* Montevecchi, W.A. & Gaston, A.J., *eds. Studies of high-latitude seabirds.* vol.1. Dartmouth: Canadian Wildlife Service, 9–15.

Casaux, R. & Barrera-Oro, E.R. 2006. Review. Shags in Antarctica: their feeding behaviour and ecological role in the marine food web. *Antarctic Science*, **18**, 3–14.

Casaux, R., Mazzotta, A. & Barrera-Oro, E. 1990. Seasonal aspects of the biology and diet of nearshore Nototheniid fish at Peter Cove, South Shetland Islands, Antarctica. *Polar Biology*, **11**, 63–72.

Casaux, R., Favero, M., Silva, P. & Baroni, A. 2001. Sex differences in diving depths and diet of Antarctic shags at the South Shetland Islands. *Journal of Field Ornithology*, **72**, 22–29.

Childress, R.B. & Bennun, L.A. 2002. Sexual character intensity and its relationship to breeding timing, fecundity and mate choice in the great cormorant *Phalacrocorax carbo lucidus*. *Journal of Avian Biology*, **33**, 23–30**.**

Cook, T.R., Cherel, Y. & Tremblay, Y. 2006. Foraging tactics of chick-rearing Crozet shags: individuals display repetitive activity and diving patterns over time. *Polar Biology*, **29**, 562–569.

Croxall, J.P., Naito, Y., Kato, A., Rothery, P. & Briggs, D.R. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *Journal of Zoology*, **225**, 177–199.

Derenne, P., Mary, G. & Mougin, J.L. 1976. Le cormoran à ventre blanc *Phalacrocorax albiventer melanogenis* (Blyth) de l'archipel Crozet. *Comité National Français de Recherche Antarctique*, **40**, 149–175.

Fairbairn, J. & Shine, R. 1993. Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. *Oikos*, **68**, 139–145.

Favero, M., Casaux, R., Silva, P., Barrera-Oro, E. & Coria, N. 1998. The diet of the Antarctic shag during summer at Nelson Island, Antarctica. *Condor*, **100**, 112–118.

Gon, O. & Heemstra, P.C. 1999. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 462 pp.

González-Solís, J., Croxall, J.P. & Wood, A.G. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels *Macronectes halli* during incubation. *Oikos*, **90**, 390–398.

Green, K. & Williams, R. 1997. Biology of the Heard Island shag *Phalacrocorax nivalis*. 3. Foraging, diet and diving behaviour. *Emu*, **97**, 76–83.

Ihaka, R. & Gentleman, R. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.

Ishikawa, K. & Watanuki, Y. 2002. Sex and individual differences in foraging behaviour of Japanese cormorants in years of different prey availability. *Journal of Ethology*, **20**, 49–54.

Jones, I.L., Rowe, S., Carr, S.M., Fraser, G. & Taylor, P. 2002. Different patterns of parental effort during chick-rearing by female and male thick-billed murres (*Uria lomvia*) at a low-Arctic colony. *Auk*, **119**, 1064–1074.

Kato, A., Nishiumi, I. & Naito, Y. 1996. Sexual differences in the diet of king cormorants at Macquarie Island. *Polar Biology*, **16**, 75–77.

Kato, A., Watanuki, Y. & Naito, Y. 1998. Benthic and pelagic foraging of two Japanese cormorants, determined by simultaneous recording of location and diving activity. *Journal of the Yamashina Institute of Ornithology*, **30**, 101–108.

Kato, A., Croxall, J.P., Watanuki, Y. & Naito, Y. 1992. Diving patterns and performance in male and female blue-eyed cormorants *Phalacrocorax atriceps* at South Georgia. *Marine Ornithology*, **19**, 117–129.

Kato, A., Watanuki, Y., Shaughnessy, P., Le Maho, Y. & Naito, Y. 1999. Intersexual differences in the diving behaviour of foraging subantarctic cormorant (*Phalacrocorax albiventer*) and Japanese cormorant (*P. filamentosus*). *Compte Rendu de l'Académie des Sciences de Paris*, **322**, 557–562.

KATO, A., WATANUKI, Y., NISHIUMI, I., KUROKI, M., SHAUGHNESSY, P. & NAITO, Y. 2000. Variation in foraging and parental behavior of king cormorants. *Auk*, **117**, 718–730.

KOFFIJBERG, K. & VAN EERDEN, M. 1995. Sexual dimorphism in the cormorant *Phalacrocorax carbo sinensis*: possible implications for differences in structural size. *Ardea*, **83**, 37–46.

KOOYMAN, G.L. & KOOYMAN, T.G. 1995. Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor*, **97**, 536–549.

LEWIS, S., BENVENUTI, S., DALL'ANTONIA, L., GRIFFITHS, R., MONEY, L., SHERRATT, T.N., WANLESS, S. & HAMER, K.C. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London*, **B269**, 1687–1693.

LORMÉE, H., JOUVENTIN, P., TROUVÉ, C. & CHASTEL, O. 2003. Sex-specific patterns in baseline corticosterone and body condition changes in breeding red-footed boobies, *Sula sula*. *Ibis*, **145**, 212–219.

MALACALZA, V.E. & HALL, M.A. 1988. Sexing adult king cormorants (*Phalacrocorax albiventer*) by discriminant analysis. *Colonial Waterbirds*, **11**, 32–37.

MILLER, R.G. 1993. *History and atlas of the fishes of the Antarctic Ocean*. Carson City: Foresta Institute for Ocean and Mountain Studies, 792 pp.

ORTA, J. 1992. Family Phalacrocoracidae (Cormorants). *In* DEL HOYO, J., ELLIOTT, A. & SARGATAL, J., *eds. Handbook of the birds of the world.* vol. 1. Barcelona: Lynx Edicions, 326–353.

PATTERSON, H.D. & THOMPSON, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika*, **58**, 545–554.

SCHALL, R. 1991. Estimation in generalised linear models with random effects. *Biometrika*, **78**, 719–727.

SCHREER, J.F. & KOVACS, K.M. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology*, **75**, 339–358.

SELANDER, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor*, **68**, 113–151.

SHAFFER, S.A., WEIMERSKIRCH, H. & COSTA, D.P. 2001. Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Functional Ecology*, **15**, 203–210.

SMITH, T.B. 1987. Bill size polymorphism and interspecific niche utilisation in an African finch. *Nature*, **329**, 717–719.

SPEAR, L.B. & AINLEY, D.G. 1997. Flight speed of seabirds in relation to wind speed and direction. *Ibis*, **139**, 234–251.

TREMBLAY, Y. & CHEREL, Y. 2000. Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Marine Ecology Progress Series*, **204**, 257–267.

TREMBLAY, Y. & CHEREL, Y. 2003. Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Marine Ecology Progress Series*, **251**, 279–297.

TREMBLAY, Y., COOK, T.R. & CHEREL, Y. 2005. Time budget and diving behaviour of chick-rearing Crozet shags. *Canadian Journal of Zoology*, **83**, 971–982.

TREMBLAY, Y., CHEREL, Y., OREMUS, M., TVERAA, T. & CHASTEL, O. 2003. Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *Journal of Experimental Biology*, **206**, 1929–1940.

WANLESS, S., HARRIS, M.P. & MORRIS, J.A. 1992. Diving behaviour and diet of blue-eyed shags at South Georgia. *Polar Biology*, **12**, 713–719.

WANLESS, S., HARRIS, M.P. & MORRIS, J.A. 1995. Factors affecting daily activity budgets of South Georgian shags during chick rearing at Bird Island, South Georgia. *Condor*, **97**, 550–558.

WATANUKI, Y., KATO, A. & NAITO, Y. 1996. Diving performance of male and female Japanese cormorants. *Canadian Journal of Zoology*, **74**, 1098–1109.

WEIMERSKIRCH, H., SALAMOLARD, M., SARRAZIN, F. & JOUVENTIN, P. 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**, 325–342.

WHITE, M.G. 1998. Development, dispersal and recruitment: a paradox for survival among Antarctic fish. *In* DI PRISCO, G., PISANO, E. & CLARKE, A., *eds. Fishes of Antarctica, a biological overview.* Milan: Springer, 53–62.