ORIGINAL PAPER

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Foraging tactics of chick-rearing Crozet shags: individuals display repetitive activity and diving patterns over time

Abstract It is in the interest of resident and long-lived benthic foragers to learn to apply efficient foraging tactics throughout their lifetime, thus increasing their individual efficiency. To test whether individuals are capable of applying an individual-specific foraging pattern, we checked for the existence of established foraging routines. Using ventrally attached time-depth recorders, we studied the individual foraging tactics of chick-rearing Crozet shags (*Phalacrocorax melanogenis*, Blyth 1860), as measured by the consistency in individual daily activity patterns and diving profiles over time. Individuals displayed a fidelity to the time of first daily trip to sea and also a strong fidelity to one, two or three depth ranges day after day. We suggest foraging area fidelity, a behaviour that could help increase foraging efficiency thanks to the memorization of the bottom's topography and the habits of its fauna, as a hypothesis for explaining some of these patterns. We propose the question of foraging area fidelity should be more specifically addressed in the future.

Introduction

Seabirds and non-cetacean marine mammals have very distinct areas for breeding (on land), and for feeding (at sea). Consequently, they face a permanent challenge, which has shaped their life histories (Ashmole 1971; Fiedler 2002): how to find mobile food in the immensity

of the ocean ecosystem. To understand how they manage foraging in the marine environment, researchers have devoted considerable effort in recent years to understanding the foraging ecology of marine mammals and seabirds (Jouventin and Weimerskirch 1990; Wilson et al. 1992; Costa 1993).

Nevertheless, individual foraging behaviour of marine top predators has been poorly investigated, mainly because it implies studying individuals over time (longitudinal studies), and researchers generally focus their work at a species or population level (cross-sectional studies: Bolnick et al. 2002; Tremblay and Cherel 2003). Studies on foraging thus tend to define the range of the niche that is optimal for the population (Krebs and Davies 1987). One of the reasons for this bias toward cross-sectional studies comes from the statistical sword of Damocles: "individual observations are meaningless". Yet, many species are in fact composed of individual specialists that use small subsets of the population's niche. A key characteristic of individual specialization is the repetition of a specific behaviour and/or diet over time (Amundsen et al. 1997; Estes et al. 2003). This was described in a variety of species, on both a dietary and/or a behavioural level (see Bolnick et al. 2003 for review). Specialization by individuals has been shown not only to avoid competition between conspecifics, but also to considerably increase individual efficiency in finding food through learning processes (e.g. in insects and fish: Heinrich 1976; Werner et al. 1981).

The main challenge for an individual in finding food in the ocean is suspected to be food predictability. Seabirds generally rely on more or less predictable oceanic features associated with food availability such as fronts, upwellings, or continental shelves (Hunt 1991). These features are obviously more predictable when they are static rather than when they are dynamic. Some species of marine mammals and diving seabirds target benthic or epibenthic prey (e.g. cormorants, penguins, sea lions, respectively, Orta 1992; Tremblay and Cherel 2000; Costa and Gales 2003), and thus it is reasonable to assume they may rely on topographic cues to find their

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prey. Topographic cues give individuals the possibility of memorizing the location and quality of distinct foraging grounds on a very precise scale, which is virtually impossible to do using dynamic cues.

Crozet shags (*Phalacrocorax melanogenis*, Blyth 1860) are non-migratory benthic foragers, which capture essentially benthic fish during the breeding season (Ridoux 1994). At Possession Island, Crozet Archipelago, they dive very close to the colony (within a mean range of 1–2 km), where the sea bottom falls away quickly from the coast, reaching 200 m in depth after only ≈5 km. The Crozet shags work hard during chick-rearing compared to other species of cormorants, and exhibit sexual differences in their foraging ecology, males diving deeper, foraging in different areas, eating different prey sizes, spending daily less time underwater, or having different activity schedules compared to females (Tremblay et al. 2005; Cook et al. unpublished), possibly as a consequence of intra-specific competition or food limitation.

Being resident and long-lived benthic foragers, individual Crozet shags should learn to apply efficient foraging tactics throughout their lifetime, thus increasing their individual efficiency when foraging under situations of competition or food limitation (Estes et al. 2003). In this perspective, we tested whether individuals were indeed capable of elaborating a foraging strategy (or tactic), in the sense of applying a particular foraging pattern. To do so, we checked for the existence of established foraging routines in individual chick-rearing Crozet shags by measuring day to day individual activity patterns and diving depths using time-depth recorders (TDR MK7 Wildlife Computers, Woodinville, Washington, USA).

Materials and methods

Study site, birds and general procedure

Field work was conducted between the 28 of January and the 9 of February 1999 at Pointe Basse (46°21′S, 51°42′E), Possession Island, Crozet Archipelago (Local Time: UTC + 3h20) in a small colony of Crozet shags (13 nests).

Twelve individuals (six males and six females from six pairs) of Crozet shags were studied during the chick-rearing period (1.8 ± 0.7 chicks per nest, age of chicks between 10 and 50 days). The birds were captured at night by hand (both partners are then present at the nest), and weighed (precision ± 25 g) using a spring balance, measured for sexing (Malacalaza and Hall 1988), and a TDR was attached ventrally according to Tremblay et al. (2003) for a 4–6 day deployment period, using cyanoacrylate glue (Loctite 401) and plastic ties (total initial handling time ≈5 min). At the end of the study period, loggers were retrieved at a moment when birds came back from the sea (immediately after return to the nest).

The TDRs were 8.6×2.0×1.1 cm^3, and weighed 27 g, corresponding to ≈1.1% of the birds' mean body mass. Recorder tips were streamlined to reduce drag. The pressure and light sensors reacted immediately to changes in the environment, while the temperature sensor had a longer reaction time: TDRs were therefore programmed to record depth and light every 1 s and external temperature every 5 s. Depth and temperature resolution were ± 1 m and ± 0.1°C, respectively. Light (arbitrary scale) was linearly related to $\log_{10}$lx (Wanless et al. 1999). Memory was 2.03 MB.

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 and statistics

Time budget analysis was performed using the advantages inherent in the ventral attachment technique (Tremblay et al. 2003). Foraging trips and flights were determined by simultaneous reading of depth, light, and temperature profiles in relation to time (for details on the procedure at Crozet, see Tremblay et al. 2005). Using our own designed software for dive analysis (see for example Tremblay and Cherel 2000, 2003), analysis of dive profiles was performed in order to gather dive depths for every individual. Mean bird flight speeds were assumed 58 km/h (Spear and Ainley 1997).

Individual foraging behaviours were compared from 1 day to the next, in order to determine possible established and repeated patterns, suggesting individual tactics. Time of first departure to sea was compared day to day, over a period of 4–6 days. Mean daily flight duration for all daily trips (to commute to the sea surface and to come back to the colony) was compared to daily mean dive depth over 4–5 days (in order to use days with full daily data on foraging activity). Daily mean and maximum dive depths were examined in the same manner, and dive frequencies in relation to dive depth were compared on a daily basis.

Finally, the data were analysed statistically using the non-parametric Spearman rank correlation test (to test the effect of different variables on the departure time of birds), and regressions otherwise, when data permitted it. Software used was STATISTICA 6.1 (Copyright© StatSoft, Inc. 1984–2004) and SIGMAPLOT 8.0 (Copyright© SPSS, Inc. 1986–2001), with an α-level of significance of $P < 0.05$. The mean values are given ± SD.

Results

At sea behaviour was successfully recorded for 4–6 consecutive days in 12 Crozet shag individuals, days with full daily data ranging from 4 to 5. Detailed observation of several foraging parameters for each bird separately showed remarkable consistency over time.
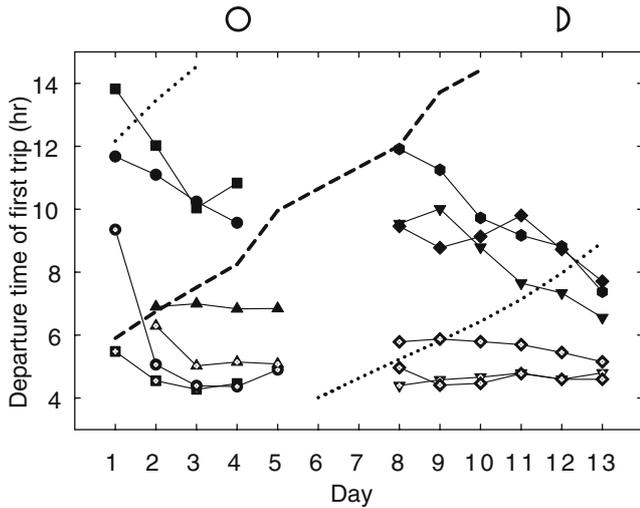
Fig. 1 Departure time of first trip of the day to sea during the study period, for all individuals. *Full black symbols* and *symbols with white crosses* represent males and females, respectively. *Identically shaped symbols* correspond to the two partners of a same nest. The *short dashed line* is the schedule of high tide, and the *dotted lines* are the schedule of low tide. Day of full moon is illustrated by a *full white circle*, and day of the last Moon quarter by a *half white circle*

Daily activity patterns

Time of first daily departure to sea was generally constant day after day for the same individual (Fig. 1). The time range was either specific to an individual, or overlapped the range of another. This time was either constant (in females and in one male), or became earlier day after day (in the other males, on average 36 ± 44 min earlier on every subsequent day compared to the day before; exponential decay: $R^2 = 0.29$, $N = 30$, $P = 0.002$). Five out of six males displayed this trend throughout the study, as did four out of six females, but only during the first or second day. The earlier departure schedules of

males over time were not explained by the daily time spent at sea (no relation between schedule and time spent at sea: $R^2 = 0.0045$, $N = 21$, $P = 0.773$). The departure time did decrease with the daily number of trips ($R^2 = 0.22$, $N = 21$, $P = 0.032$). The relation between departure time and total chick mass per nest was non-significant for males (Spearman's Rank Correlation: $R_s = 0.26$, $N = 6$, $P = 0.623$). Eventually, time of high tide occurred on average 60 ± 26 min later on every new day (Fig. 1; highest tidal range over the study period: 0.40 m). There was a negative correlation between the tide schedule and time of first departure (Spearman's Rank Correlation: $R_s = 0.48$, $N = 30$, $P = 0.006$). Finally, time spent daily at sea varied greatly from 1 day to the next for the same individual.

Dive depth and frequency

Daily mean dive depth was exceptionally constant over time for any given individual, and restricted to a specific depth range (Fig. 2; Table 1), as were individual daily maximum dive depths (Fig. 2). Individual depth ranges rarely overlapped one another. This consistency was interrupted on 1 day, but individuals came back to their favourite depth after this change (Fig. 2). There was a positive linear relationship between daily mean and daily maximum dive depth ($y = 0.4286x + 4.0461$, $R^2 = 0.53$, $N = 55$, $P < 0.0001$).

Expressed differently, dive distribution in relation to dive depth showed strong consistency from 1 day to the next. An individual was considered fully consistent when the mode of dive distribution occurred in the same depth class, day after day. Conversely, no consistency whatsoever was considered to exist when the mode of dive distribution occurred every day in a different depth class (Fig. 3). Thus, out of 12 individuals, 1 bird showed no consistent pattern in dive

Fig. 2 Daily mean and maximum dive depth in relation to day number for individual Crozet shags. For reasons of clarity, males (**a**) and females (**b**) are shown in different panels
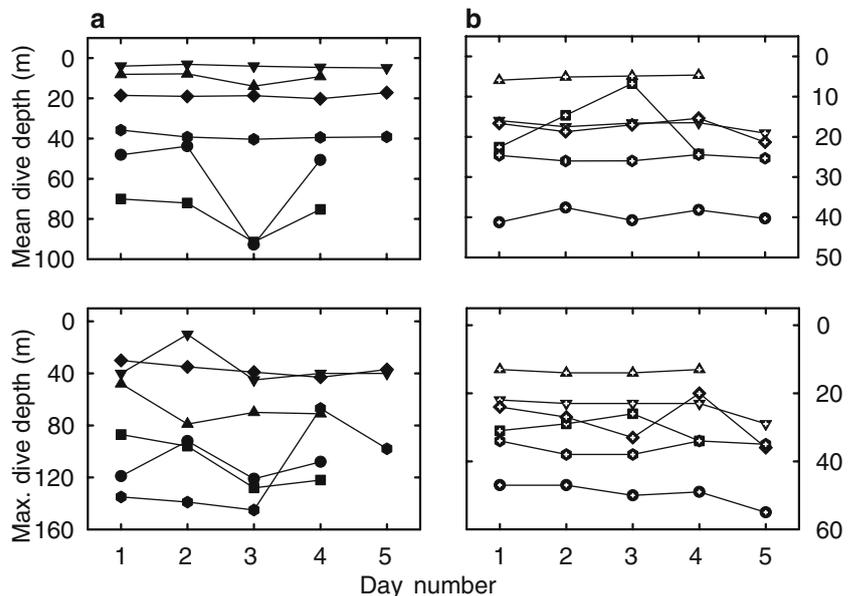
Table 1 Mean daily dive depth ($\pm$SD) for every bird over the study period for days with full daily diving data

Day	Bird (sex)											
	1 (M)	2 (M)	3 (F)	4 (F)	5 (F)	6 (M)	7 (M)	8 (F)	9 (M)	10 (F)	11 (M)	12 (F)
Mean daily dive depth (m)												
1	48 ± 18	70 ± 9	23 ± 2	41 ± 5	6 ± 2	8 ± 11	4 ± 4	17 ± 3	19 ± 5	16 ± 2	36 ± 21	25 ± 5
2	44 ± 13	72 ± 12	15 ± 9	39 ± 9	5 ± 2	8 ± 12	3 ± 1	19 ± 3	19 ± 6	17 ± 2	39 ± 22	26 ± 5
3	93 ± 21	91 ± 23	7 ± 7	41 ± 11	5 ± 2	14 ± 20	4 ± 6	17 ± 4	19 ± 8	17 ± 2	40 ± 25	26 ± 5
4	51 ± 28	75 ± 27	24 ± 3	38 ± 8	5 ± 2	9 ± 15	5 ± 3	15 ± 2	20 ± 10	16 ± 2	39 ± 14	24 ± 5
5	–	–	–	44 ± 8	–	–	5 ± 5	21 ± 5	17 ± 7	19 ± 3	39 ± 14	25 ± 4

M Male; *F* Female

distribution over time (bird A, Fig. 3). Of the 11 remaining, 2 birds showed a consistent pattern associated with an alternative mode of dive distribution occurring on 1 day out of four, and 9 birds showed a fixed mode over all study days. All these nine birds consistently used one major depth range, and sometimes one, or two minor additional depth ranges (Figs. 3, 4, 5).

Finally, daily mean dive depth was positively related to daily mean flight duration commuting out to sea from the colony ($y = 0.51x + 44.21$, $R^2 = 0.16$, $N = 55$, $P = 0.003$).
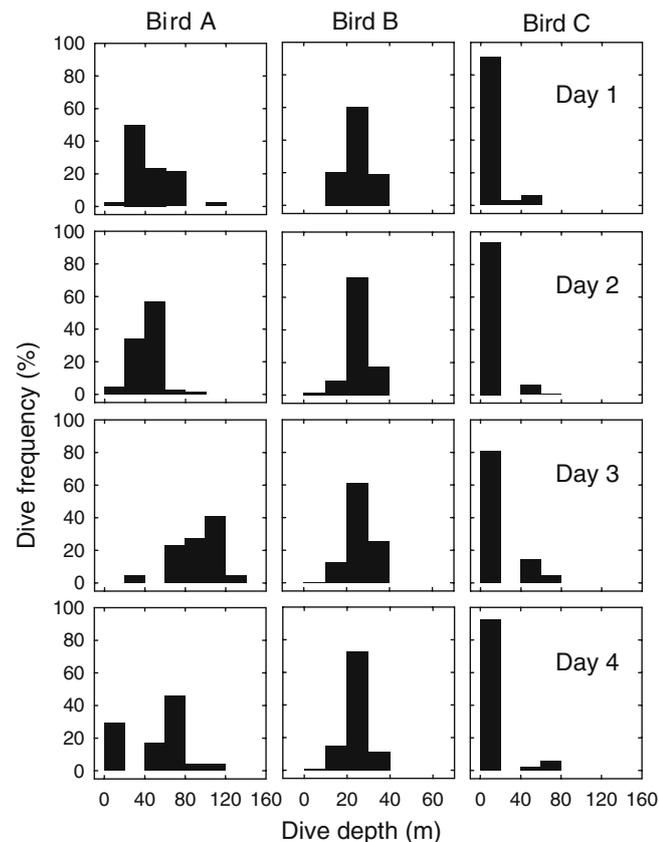
Dive type combinations

Another level of individual diving consistency was found in the daily temporal pattern of diving. Some individuals tended to alternate bouts and/or trips at similar time intervals from 1 day to the next. Diving patterns over 6 days of a male and a female from the same nest are given in Figs. 4 and 5, respectively. The male exhibited
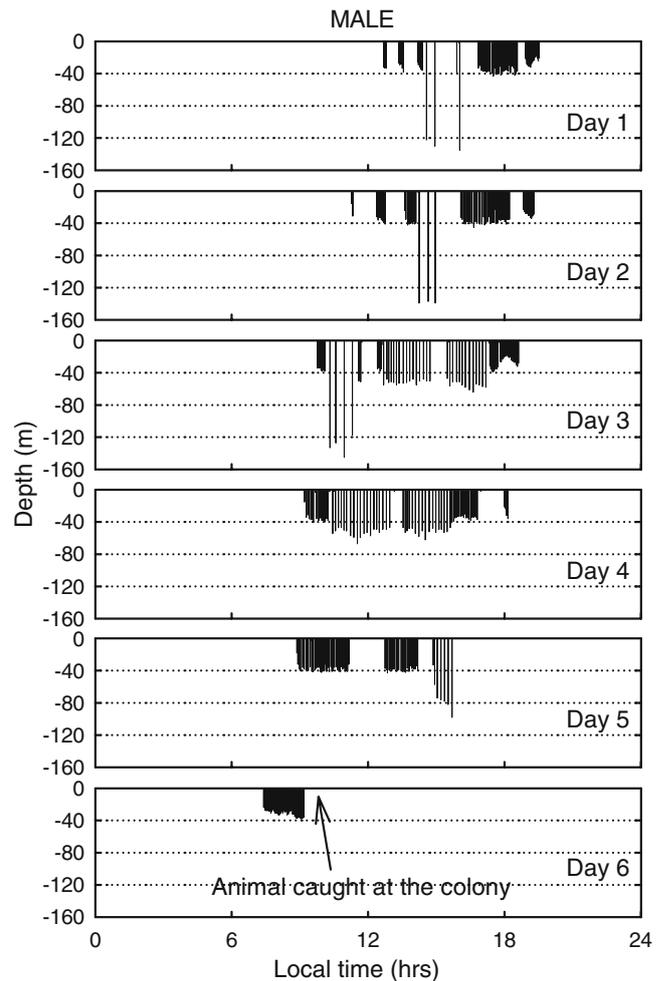

Fig. 3 Selected dive distribution in relation to dive depth for three Crozet shags over 4 days. Two patterns are represented. For bird **a** (a male), the mode of dive frequency was different every day (8% of birds). For bird **b** (a female), and bird **c** (a male), the mode of dive frequency was mostly consistent day after day (92% of birds). In **c**, a second mode is visible in a depth class which is quite separate from the first

Fig. 4 Diving pattern of a male Crozet shag over 6 days. The corresponding diving pattern of the female of the same nest is given in Fig. 5
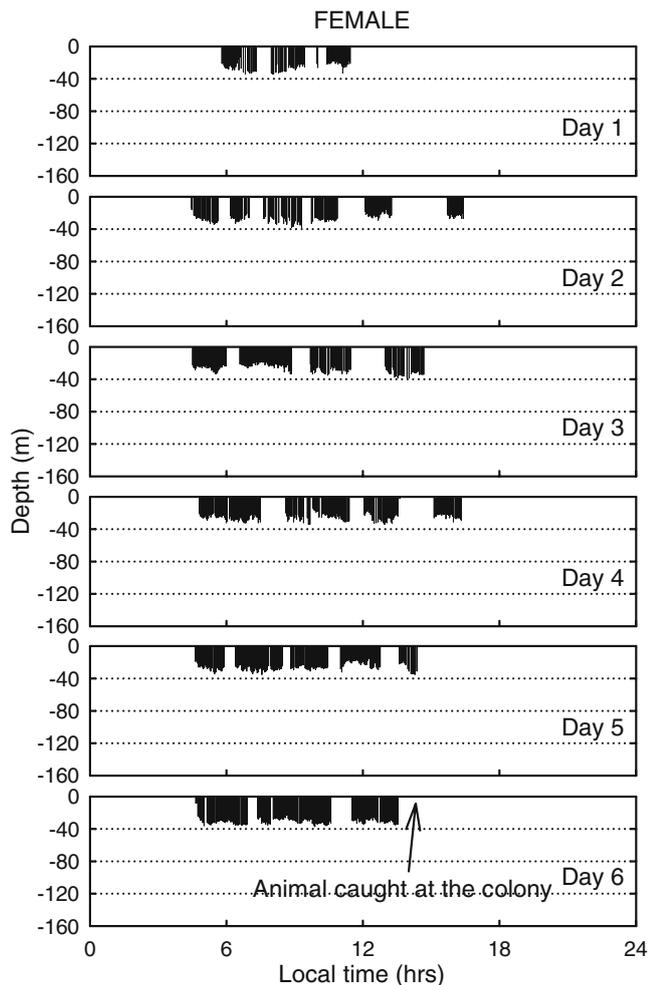
Fig. 5 Diving pattern of a female Crozet shag. The corresponding diving pattern of the male of the same nest is given in Fig. 4

nearly the same exact diving pattern on day 1 and day 2. Two dive types are found in these 2 days: type 1 between 30 and 40 m and type 2 over 120 m. The order of the sequence is type 1, type 2, and type 1. On day 3, the male repeated this sequence, and introduced type 3 dives, between 60 and 80 m. On day 4, the male repeated the sequence of the preceding day, omitting type 2 dives. On day 5, the male repeated again the preceding day's sequence, but in another order: type 1, type 1, type 3, instead of type 1, type 3, and type 1. During 6 days, this male always started its first bouts by type 1 dives. The female only used type 1 dives, which she repeated during 66 consecutive bouts over 6 days. Thus, some individuals have a certain repertoire of dive types, which they combine in various orders, sometimes in a very consistent manner. This was obvious for less than half of all individuals, and difficult to see in others. There was no clear difference between the sexes.

Eventually, when at sea (4.4 ± 0.9 trips/day) birds flew 1.5 ± 0.6 times per trip (flights occurred between dive bouts), not counting flights commuting from the colony to the ocean or back, and including trips where no dives were carried out (6.6%). These flights,

sometimes separating entirely different depth ranges, lasted on average 72 ± 71 s.

Discussion

Blue-eyed shags can display shifts in diet (Green and Williams 1997), forage alone or in groups (Derenne et al. 1976), are benthic divers, but can also carry out some pelagic dives (Tremblay et al. 2005), and exhibit sex-specific foraging behaviour (Kato et al. 1996; Cook et al., unpublished). In addition, we have shown here for the first time the presence of individual-specific foraging habits in the Crozet shag.

Foraging schedule

Most individuals preferred a certain time for first departure of the day (Fig. 1). Some birds were, however, more constant than others, respecting a tight time range day after day. The daily number of trips decreased with departure time, but this was compensated by the time spent at sea, which did not vary significantly. Male timing would appear dependent on female timing because females start fishing earlier in the morning (Cook et al., unpublished). Yet, most chicks were already thermally emancipated during the study period, and birds showed fidelity to individual time ranges, indicating they were largely conditioned by individual habits, independent of nest shift schedules. Individual fidelity to a foraging depth range could be a factor determining departure time. Indeed, blue-eyed shags, because they need light to spot their prey underwater, are very sensitive to light levels (Wanless et al. 1999). The colony is on a part of the island where the coast is jagged and sinuous and lined with high cliffs. Consequently, in the morning, some coastal waters are in the sun, while others, not far away, are still in the shade. A cormorant might try to commute to the feeding site as soon as it is touched by the sun, which would be about at the same time every day. This could explain why the females are so constant in their departure times compared to the males. Males would be less sensitive to the influence of coast morphology, because the sun is already high in the sky when they start foraging. It remains difficult to explain why most males left every day earlier than the day before. Increasing earliness of departure was not related to an increase in time spent at sea or to a growing number of trips. Earlier departure times were correlated to later high tide schedules, thus the complete opposite of the prediction that birds might have synchronized their departure schedule with a particular tide level or with the coming or the going of the tide, day after day. The premise of an effect of the tide on the daily activity patterns of the Crozet shag appears tenuous as the tidal range varies between 0.10 and 0.40 m and the sea bottom falls away quickly from the shore. Equipping birds over a longer period (e.g. 1 month), would help tackle this issue.

Finally, there was little consistency in the time spent at sea from 1 day to the next for the same individual, though females spent more time overall diving compared to males (3 h/day vs. 2 h for the males, Cook et al., unpublished).

Dive depth fidelity

Individual fidelity to a restricted diving depth range was extremely high (Fig. 2). Out of the 12 individuals, 75% showed fidelity to one or two depth ranges, 17% showed fidelity to one depth range, then changed on 1 day, before coming back, and 8% changed depth range every day. When not fixed, we observed that differences in depth distribution between days potentially resulted from individuals displaying various but individual-specific types of dives in different orders from day to day.

Because Crozet shags feed benthically (Tremblay et al. 2005), we propose foraging fidelity to a specific food patch (Grémillet et al. 1999) as a hypothesis helping to explain fidelity to a precise depth range. This behaviour could be consistent with the fidelity to the departure time in our study birds. In terms of efficiency, returning to a known area would be logical if a satisfactory amount of prey items is found the first time. Memory of the underwater bottom topography would be determinant in foraging success. This would be true for a benthic diver like the cormorant, particularly when it feeds on a rocky seabed as is the case here, where visual landmarks are certainly important for orientation. Repeated exploration of a same feeding site might allow memorization of the surroundings, increasing the efficiency of prey localization and capture. Daily mean flight duration commuting out to sea from the colony was positively related to daily mean dive depth, suggesting animals could fly directly over to a favourite zone (within a range of depths), which they would exploit throughout the day, jointly with other secondary minor areas. Foraging area fidelity has been suggested in some seabird species, such as for example shags *Phalacrocorax filamentosus* (Watanuki et al. 2004), gulls *Rissa tridactyla* (Irons 1998), penguins *Eudyptula minor* (Ropert-Coudert et al. 2003), and *Pygoscelis adeliae* (Watanuki et al. 2003), or gannets *Morus bassanus* (Hamer et al. 2001).

The difficulty and importance of studying individual foraging behaviour

Though dive depth fidelity is probably related to foraging area fidelity in the Crozet shag, future confirmation on feeding location fidelity will be necessary through other methods which measure spatial parameters. Actually measuring such parameters at such a small scale (only a few hundred metres to move from shallow waters to waters 100 m deep) is challenging. Indeed, it usually requires complex methods, such as Global Positioning System, to measure location on coastal seabirds which display such limited movement. Though possible (Grémillet et al. 2004), to date, it still remains difficult to fit GPS data loggers on shags. First for financial reasons, but also for technical reasons, such as the weight of the GPS, the waterproof quality of the logger when the shag is diving to great depths, or the length of the surface periods, the only time when contact with a satellite is possible. At sea radio-telemetry is a more classical solution, but must be used cautiously when birds forage at a very small scale (as in this study: mean foraging range < 2 km), because it lacks accuracy (accuracy 0.5–2.0 km, more rarely 0.2 km see for example Wanless and Harris 1993; Kato et al. 1998; Grémillet et al. 1999; Watanuki et al. 2003; Anderson et al. 2004). It has nevertheless been used successfully on cormorants with reduced foraging ranges (Quintana 2001; Sapoznikow and Quintana 2003; Quintana et al. 2004). These authors showed on the imperial cormorant *Phalacrocorax atriceps*, the rock shag *Phalacrocorax magellanicus*, and the neotropic cormorant *Phalacrocorax brasilianus* an almost exclusive utilization of the same feeding area during a same foraging trip for any given individual. The authors have also described for certain individuals a minor utilization of one or several secondary areas, a behaviour in a way similar to the minor utilizations of secondary depth ranges by the Crozet shags in the present study. Our birds flew between these depth zones during ≈1 min on average, thus potentially travelling between zones separated by approximately 1 km in a straight line. In the future, consistency in feeding locations should be addressed in Crozet shags by using for example radio-telemetry (simultaneously or not to time-depth recorders), to test the fidelity of individuals to feeding patches. For example, as suggested here (Figs. 3, 4, 5), when birds possess several foraging areas (one major, and one or two minors), do they visit them daily in the same order, and if so, what does it mean? More importantly, fidelity should be tested over a period of several days, but also of several years, as this species is highly philopatric (Derenne et al. 1976).

The ecological causes and consequences of individual habits are poorly documented, although some studies have tackled the issue. For example, in the coastal diving pigeon guillemot *Cepphus columba*, individuals with a specialized diet had higher fledging rates than generalists (Golet et al. 2000). In breeding great cormorants, Voslamber et al. (1995) observed that individual specialists (solitary foragers vs. group foragers) were more efficient in capturing fish and captured more than non-specialized individuals. These specialists were probably more experienced, suggesting individuals might start as generalists when they are young, and specialize with age, acquiring food with more efficiency (Greig et al. 1983).

Conclusions

Individual habits are therefore an important aspect in the foraging behaviours of breeding Crozet shags, independently from the sex, and foraging area fidelity

could be a predominant behaviour. The cognitive process in individual foraging strategies should be important in the selection of a pattern, with memory of the patch location and quality playing an essential role, probably mixed with other processes, such as cueing to the activities of conspecifics (local enhancement, Davoren et al. 2003). Living over a period of time in a zone where it is possible to recognize a particular area or bottom topography as being associated with various amounts of prey would offer the perfect conditions for memorizing patch location and quality. We suspect this strategy enables considerably reducing search time among marine predators by enhancing the predictability of prey location for a given individual. We would expect this strategy to be used among all benthic top predators, especially by individuals of resident species.

The effect of various degrees of consistency in diving patterns on reproductive success could be addressed in the Crozet shags. At this stage, our data only describe a previously undocumented example of individual habits at a behavioural—not diet—level. As pointed out by Bolnick et al. (2003), many questions remain to be investigated in the field of individual specialization, as for example the persistence over time of the habits throughout the life cycle, and the effect of density dependence on the degree of specialization in various populations (Estes et al. 2003). Benthic divers offer an excellent opportunity for studying individual specialization, and we propose that longitudinal studies should be conducted on a more systematic basis.

References

Amundsen P-A, Siikavuopio S, Christensen G (1997) Significance and temporal persistence of individual specialization in cannibalistic Arctic char, *Salvelinus alpinus*. Nord J Fresh Res 73:28–34

Anderson CD, Roby DD, Collins K (2004) Foraging pattern of male and female double-crested cormorants nesting in the Columbia River estuary. Can J Zool 82:541–554

Ashmole NP (1971) Seabird ecology and the marine environment. In: Farner DS, King JR (eds) Avian biology, vol 1. Academic, New York, pp 223–286

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. Ecology 83:2936–2941

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28

Costa DP (1993) The secret life of marine mammals: novel tools for studying their behaviour and biology at sea. Oceanography 6:120–128

Costa DP, Gales NJ (2003) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol Monogr 73:27–43

Davoren GK, Montevecchi WA, Anderson JT (2003) Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecol Monogr 73:463–481

Derenne P, Mary G, Mougin JL (1976) Le cormoran à ventre blanc Phalacrocorax albiventer melanogenis (Blyth) de l'archipel Crozet. Comité Natl Français Rech Ant 40:149–175

Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. J Anim Ecol 72:144–155

Fiedler PC (2002) Ocean environment. In: Perrin WF, Wursig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic, San Diego, pp 824–830

Golet GH, Kuletz KJ, Roby DD, Irons DB (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. Auk 117:82–91

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

Greig SA, Coulson JC, Monaghan P (1983) Age-related differences in foraging success in the herring gull (*Larus argentus*). Anim Behav 31:1237–1243

Grémillet D, Wilson RP, Storch S, Gary Y (1999) Three-dimensional space utilisation by a marine predator. Mar Ecol Prog Ser 183:263–273

Grémillet D, Dell'Omo G, Ryan PG, Peters G, Ropert-Coudert Y, Weeks SJ (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. Mar Ecol Prog Ser 268:265–279

Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of gannets Morus bassanus at two North Atlantic colonies: foraging trip duration and foraging area fidelity. Mar Ecol Prog Ser 224:283–290

Heinrich B (1976) The foraging specializations of individual bumblebees. Ecol Monogr 46:105–128

Hunt GL Jr (1991) Marine ecology of seabirds in polar oceans. Am Zool 31:131–142

Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79:647–655

Jouventin P, Weimerskirch H (1990) Satellite tracking of wandering albatrosses. Nature 343:746–748

Kato A, Nishiumi I, Naito Y (1996) Sexual differences in the diet of king cormorants at Macquarie Island. Polar Biol 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. J Yamashina Inst Ornithol 30:101–108

Krebs JR, Davies NB (1987) An introduction to behavioural ecology. Blackwell, Oxford

Malacalaza VE, Hall MA (1988) Sexing adult king cormorants (*Phalacrocorax albiventer*) by discriminant analysis. Col Waterbirds 11:32–37

Orta J (1992) Family Phalacrocoracidae (Cormorants). In: Del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world, 1. Lynx Edicions, Barcelona, pp 326–353

Quintana F (2001) Foraging behaviour and feeding locations of Rock Shags Phalacrocorax magellanicus from a colony in Patagonia, Argentina. Ibis 143:547–553

Quintana F, Yorio P, Lisnizier N, Gatto A, Soria G (2004) Diving behaviour and foraging areas of the neotropic cormorant at the marine colony in Patagonia, Argentina. Wilson Bull 116:83–88

Ropert-Coudert Y, Kato A, Naito Y, Cannell BL (2003) Individual diving strategies in the little penguin. Waterbirds 26:403–408

Ridoux V (1994) The diets and dietary segregation of seabirds at the sub-Antarctic Crozet islands. Mar Ornithol 22:1–192

Sapoznikow A, Quintana F (2003) Foraging behaviour and feeding locations of imperial cormorants and rock shags breeding sympatrically in Patagonia, Argentina. Waterbirds 26:184–191

Spear LB, Ainley DG (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. Mar Ecol Prog Ser 204:257–267

Tremblay Y, Cherel Y (2003) Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. Mar Ecol Prog Ser 251:279–297

Tremblay Y, Cook TR, Cherel Y (2005) Time budget and diving behaviour of chick-rearing Crozet shags. Can J Zool 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. J Exp Biol 206:1929–1940

Voslamber B, Platteeuw M, Van Eerden MR (1995) Solitary foraging in sand pits by breeding cormorants *Phalacrocorax carbo sinensis*: does specialised knowledge about fishing sites and fish behaviour pay off? Ardea 83:213–222

Wanless S, Harris MP (1993) Use of mutually exclusive foraging areas by adjacent colonies of blue-eyed shags (*Phalacrocorax atriceps*) at South Georgia. Col Waterbirds 16:176–182

Wanless S, Finney SK, Harris MP, McCafferty DJ (1999) Effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the blue-eyed shag *Phalacrocorax atriceps* and the European shag *P. aristotelis*. Mar Ecol Prog Ser 188:219–224

Watanuki Y, Takahashi A, Sato K (2003) Feeding area specialization of chick-rearing Adélie Penguins *Pygoscelis adeliae* in a fast sea–ice area. Ibis 145:558–564

Watanuki Y, Ishikawa K, Takahashi A, Kato A (2004) Foraging behavior of a generalist marine top predator, Japanese cormorants (*Phalacrocorax filamentosus*), in years of demersal versus epipelagic prey. Mar Biol 145:427–434

Werner EE, Mittelbach GG, Hall DJ (1981) The role of foraging profitability and experience in habitat use by the bluegill sunfish. Ecology 62:116–125

Wilson RP, Cooper J, Plötz J (1992) Can we determine when marine endotherms feed? A case study with seabirds. J Exp Biol 167:267–275