The Condor 97:550–558

FACTORS AFFECTING DAILY ACTIVITY BUDGETS OF SOUTH GEORGIAN SHAGS DURING CHICK REARING AT BIRD ISLAND, SOUTH GEORGIA[1]

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Abstract. Radio telemetry was used to record daily activity budgets of 26 South Georgian Shags (*Phalacrocorax georgianus*) during the chick-rearing period at Bird Island, South Georgia. There was a significant sex difference in the timing of feeding, with the female making the first trip of the day in 93% of pairs (n = 15). On average, each shag made 2.3 trips/day and was absent for a total of 6.22 hr/day. The majority of time away from the colony was spent diving (86.7%), but long recovery periods on the surface between dives and time needed to travel to the seabed resulted in only 1.06 hr/day being potentially available for prey capture. Given that these activity data were collected during a season when feeding conditions were favorable, breeding shags at Bird Island appear to have little capacity to increase the time available for prey capture. We speculate that the population may be extremely sensitive to changes in food availability. Males spent more time flying and on the sea than did females. On average, birds with broods of two or three chicks spent more time diving (6.42 hr/day) than those with broods of one (4.74 hr/day) but there was no tendency for the amount of time spent diving to increase with chick age. Although South Georgian Shags exhibited the same sexually distinct foraging patterns as Antarctic Shags *P. bransfieldensis* at a colony on the Antarctic Peninsula, their activity budgets differed radically, with shags at Bird Island spending a much greater percentage of their time away diving (86.7% compared with 8.4%).

Key words: *South Georgian Shag;* Phalacrocorax georgianus; *activity budgets; sex differences; diving.*

INTRODUCTION

Recent studies of activity patterns and foraging behavior of Antarctic and subantarctic marine birds have focused on penguins Spheniscidae and albatrosses Diomedeidae (e.g., Prince and Francis 1984, Trivelpiece et al. 1986, Williams and Rothery 1990, Croxall et al. 1993. In contrast, with a few notable exceptions (Bernstein and Maxson 1984, 1985; Croxall et al. 1991; Kato et al. 1992; Wanless et al. 1992) activity patterns of shags Phalacrocoracidae have received little attention.

Cairns (1987) proposed that variations in time budgets of marine birds would correlate with prey availability and several studies have demonstrated a link between avian activity patterns and prey abundance (e.g., Burger and Piatt 1990, Monaghan et al. 1994). In this study we used radiotelemetry to obtain the first continuous daily record of the behavior of South Georgian Shags *Phalacrocorax georgianus* during the chick-rearing period at Bird Island, South Georgia. These data were used to construct daily activity budgets in terms of the amount of time spent flying, diving, on the sea, and on land, either at the nest or in roosts away from the breeding colony. The aim of this paper is: (1) to describe the basic at-sea activity pattern of South Georgian Shags during chick rearing; (2) to investigate the effect of sex, brood size and chick age on activity budgets; and (3) to model the relationship between available foraging time and prey abundance.

The taxonomy and nomenclature of the Blue-eyed Shag group is complex and subject to considerable discussion and revision (Van Tets 1976, Siegel-Causey 1988, Marchant and Higgins 1990, Sibley and Monroe 1990). In most previously published papers, the population on South Georgia has been referred to as the Blue-eyed Shag *P. atriceps* (e.g., Croxall et al. 1991; Kato et al. 1992; Wanless et al. 1992, 1993) and thus considered part of a widespread species with breeding colonies on many subantarctic islands, southern South America and the Antarctic Peninsula south to latitude 68°S. However, some of the insular populations, including that on South Georgia,

[1] Received 7 September 1994. Accepted 19 December 1994.

are now considered specifically distinct (Siegel-Causey 1988, Marchant and Higgins 1990, Sibley and Monroe 1990). In this paper, we adopt the nomenclature given in Marchant and Higgins (1990).

METHODS

South Georgian Shags are resident on Bird Island, South Georgia (54°00'S, 38°02'W) and approximately 350 pairs breed annually (Wanless and Harris 1993). The study took place during the 1989 austral summer (between 28 December 1989 and 6 February 1990), at the colony of 32 shag pairs at Pearson Point at the extreme western end of the island.

Activity patterns were determined using radio-transmitters and a manned receiving station. Transmitters (2.0 cm^2 cross-sectional area, 19 g mass) were deployed on adults during the chick-rearing period by attachment to the birds' back feathers using water proof tape and three small plastic cable ties. Birds were sexed by body size and vocalizations (Bernstein and Maxson 1984, Shaw 1984). Twelve males and 14 females from 15 different pairs were followed; members of a pair were never monitored concurrently. The approximate hatching dates of the chicks of these birds were determined from visits made every 4–5 days to the colony, and brood size on the day the bird was followed was also recorded. Samples for male and female shags were balanced with respect to mean brood age, brood size, date followed and wind speed on the day monitored (t-tests all $t < 0.73$, all $P > 0.20$).

Radio signals from each shag were monitored for one complete day after which the bird was recaptured and its tag removed. Shags readily accepted the radio-tags and there was no evidence that carrying a device disrupted attendance patterns since the frequency with which single birds and pairs were present at nests where one adult was tagged, did not differ significantly from those where neither bird was carrying a device (Fisher Exact tests, $n = 70$ comparisons, all $P > 0.05$).

Foraging by South Georgian Shags occurs during daylight (pers. observ.). Accordingly radio signals were monitored from one hour before dawn (as determined from nautical tables) until one hour after dusk. In all cases radio-tagged birds were present in the colony when monitoring started and back in the colony when recording finished for the day. Signals were received using an 8-element yagi aerial mounted on the roof of a hide on the summit of Molly Hill, 135 m above sea level and about 1 km from Pearson Point. From changes in signal strength and characteristics, we could identify when a bird was ashore in the colony or on sea rocks, flying, or on the sea, or underwater (full details in Wanless and Harris 1992). Radiowaves on the 173 MHz frequency do not travel through seawater, hence the loss of signal when a bird was underwater was used to identify when and for how long a bird dived. During some trips diving activity was organized into a series of diving bouts. The duration of a bout was taken as the time between submergence on the first dive of a series and surfacing after the last dive. Bouts were distinguished (a) when the radio signal indicated that a bird flew or (b) when the surface interval between successive dives exceeded 12 min. This latter figure was derived from the clear inflexion point in a cumulative probability plot of all periods spent on the surface (Gentry and Kooyman 1986, Feldkamp et al. 1989). The interval between the last dive of the trip and the start of the flight back to the colony, however, was included in the diving time.

Foraging trips were defined as all periods spent away from the nest site except for the few cases where birds made very short flights to other parts of the island to collect nest-material. For each bird we calculated the following daily activity totals: (1) number of foraging trips, (2) duration of foraging trips, (3) time spent flying, (4) diving, (5) on sea not diving and (6) ashore away from the nest, (7) number of dives made and (8) time spent underwater. In a study using time-depth-recorders deployed on shags in the same colony, Croxall et al. (1991) found that, on average, during long deep dives (average duration 2.7–4.1 min) 47.5% of underwater time was spent in the bottom phase of the dive, the remainder being used for travelling down and up in the water column. During short shallow dives (< 1.3 min duration) no bottom time was distinguishable. We used these figures to estimate the time potentially available for prey capture (taken to be equivalent to 47.5% of underwater time for long dives and 100% for short dives) from the underwater time for each individual.

To investigate the influence of chick age and brood size on activity budgets, broods were classified into those where the oldest chick was aged 1–19 days old and those where the chicks were

older, and were divided into broods of one and two chicks (the three broods of three chicks were included in the two-chick broods).

Activity data obtained during the study were used to model the effects of reduced food availability on time budgets of South Georgian Shags. Elsewhere we have shown that predicted prey capture rates for these birds were very high (Wanless et al. 1992) and the inference was that feeding conditions during the 1989–1990 season were very good. We assumed that reduced food availability would result in lower prey capture rates and hence to meet their daily food requirements shags would need to increase the number of dives made per day. Accordingly for each bird we estimated what effect increasing the number of dives would have on the total time away from the nest each day, assuming that dive parameters and the amount of time spent flying, on the sea and ashore away from the colony, remained at the observed values. Since shags forage diurnally, total time away was expressed as a percentage of daylight hours. Similar calculations were also carried out to determine how the amount of time potentially available for prey capture varied as the number of dives/day increased.

Statistical tests were carried out in Minitab (Ryan et al. 1985). Times are given as hours and minutes, local time (± 1 SD in min) which is GMT minus 2 hr.

RESULTS

DAILY ACTIVITY PATTERNS

There was a marked sexual difference in daily activity (Fig. 1) with females leaving the colony significantly earlier (mean 04.33 hr ± 90.6 min) than males (09.27 ± 110 min, $t_{24} = 7.48$, $P < 0.001$) and also finishing feeding earlier (females 15.01 hr ± 166 min; males 18.25 hr ± 68 min, $t_{24} = 3.90$, $P < 0.001$). Assuming that our sexing criteria were correct, i.e., that the larger, vocal bird was the male, this pattern was reversed in one pair (the outlying points in the departure plots in Fig. 1). Despite their different feeding schedules, there was, however, no significant difference between the sexes in the total time active during the day (first departure–final return: females 10.44 ± 2.68 hr; males 8.96 ± 1.71 hr, $t_{24} = 1.7$, $P = 0.10$).

During the study period, the time of sunrise changed from 02.54 hr on 28 December to 04.09 hr on 6 February. Female departure time (excluding the individual showing the reversed pattern) became significantly later ($F_{1,12} = 10.55$, $P < 0.01$, $R^2 = 0.49$) as day length decreased. Including wind speeds as an additional explanatory variable did not significantly improve upon the simple regression. Over the same period there was a corresponding advancement in the time of sunset from 20.34 hr to 19.22 hr but there was no tendency for males to return earlier as the season progressed ($F_{1,11} = 0.10$, $P = 0.8$).

DAILY ACTIVITY BUDGETS

On average, a shag rearing chicks made 2.3 ± 0.8 feeding trips/day ($n = 26$) and was absent for a total of 6.22 ± 1.27 hr (38.5 ± 7.4% of daylight). Birds spent the majority of time away from the nest diving (86.7 ± 7.6%). Flying (0.35 ± 0.14 hr), on the sea not diving (0.18 ± 1.10 hr), and ashore away from the site (0.26 ± 0.32 hr) each accounted for <6% of the total time absent. Although individuals spent a considerable amount of time diving (5.42 ± 1.35 hr/day), on average, 61.4 ± 5.6% of the time was spent on the surface between dives and consequently underwater time accounted for only 2.07 ± 0.54 hr/day. After allowing for time spent travelling through the water column, this was further reduced to 1.06 ± 0.39 hr/day potentially available for prey capture, which represented only 17.4 ± 7.1% of the total time away.

Although the results described above provide an overall description of South Georgian Shag activity, it was clear that there was considerable individual variation in most aspects of foraging behavior. In an attempt to explain this we investigated the effects of dive type, sex, brood size, and chick age on each activity variable.

EFFECT OF DIVE TYPE

Two of the females followed exclusively made short dives (all <120 sec duration). The remaining 12 females and all the males spent at least 90% of their underwater time in dives lasting >120 sec. While there were significant differences in some dive parameters between long- and short-diving females, e.g., shorter mean dive duration ($t = 13.0$, $P < 0.001$) and higher percentage of diving time spent underwater ($t = 6.94$, $P < 0.001$), in other respects foraging activity in the two groups appeared to be similar (Table 1). The lack of statistically significant differences was

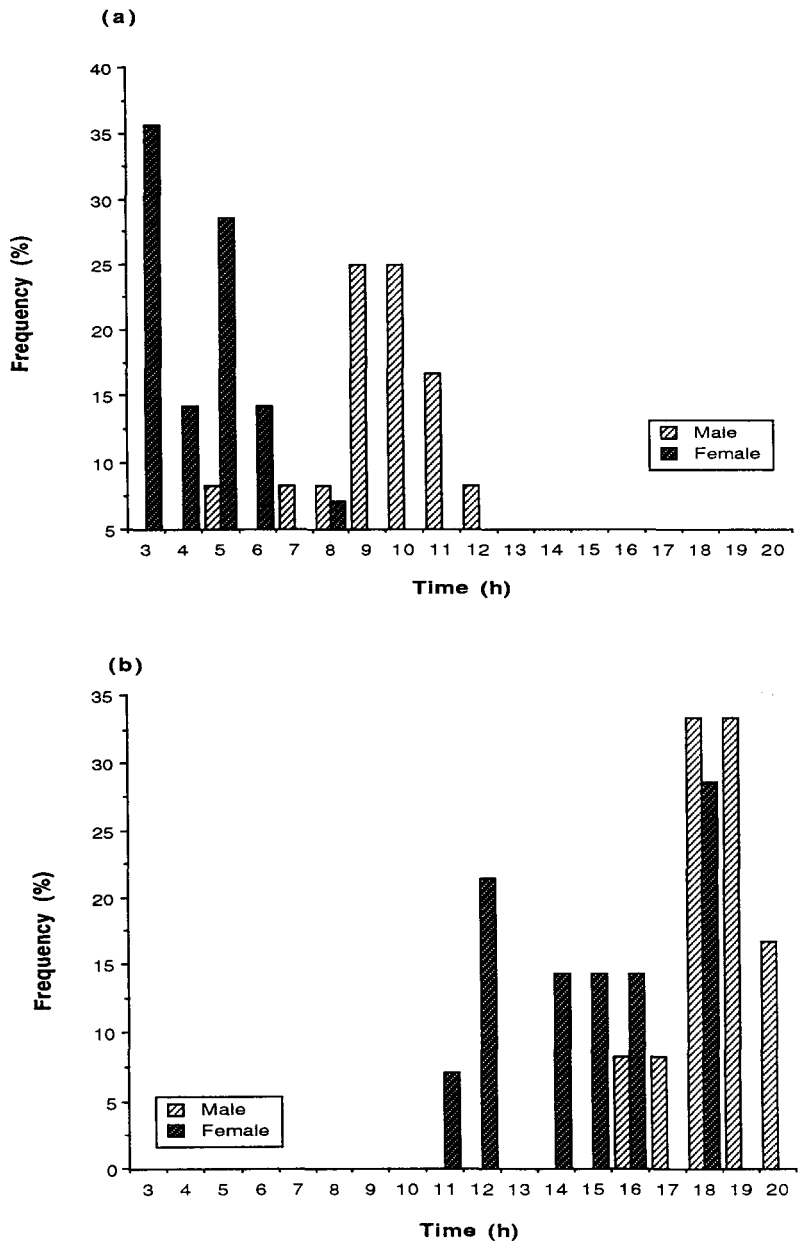

FIGURE 1. Frequency (%) distributions of (a) departure times for the first trip of the day and (b) return times after the final trip for 12 male and 14 female South Georgian Shags rearing chicks on Bird Island.

probably due to the very small sample size of short diving females (n = 2), and there was a suggestion that, although the total amount of time spent diving by individuals making short dives was less than those making long dives, the amount of time potentially available for prey capture was actually greater.

EFFECT OF SEX

The mean number of trips made per day did not differ between the sexes (t-test, $P > 0.10$) but males were away for longer than females with the difference approaching statistical significance ($t = 1.97$, $P = 0.06$, Table 2). This inequality was

TABLE 1. Characteristics of daily foraging activity (mean ± SD) for female South Georgian Shags making short and long dives.

Activity variable	Short dives (n = 2)	Long dives (n = 12)
Trip frequency (trips/day)	2.5 ± 0.7	2.5 ± 1.1
Total time away (hr)	5.12 ± 0.16	5.82 ± 1.36
Time flying (hr)	0.21 ± 0.13	0.28 ± 0.06
Time on sea (hr)	0.16 ± 0.18	0.14 ± 0.06
Time ashore away from the nest (hr)	0.72 ± 0.90	0.18 ± 0.15
Time diving (hr)	4.02 ± 1.38	5.22 ± 1.40
Time underwater (hr)	1.98 ± 0.69	2.04 ± 0.57
Percent time diving underwater	49.0 ± 0.4	39.2 ± 4.8
Estimated available prey capture time (hr)	1.98 ± 0.69	0.97 ± 0.27
Dive duration (sec)	65.9 ± 1.9	196.3 ± 34.4
Dive frequency (dives/day)	107.5 ± 34.6	39.2 ± 16.9

largely explained by males spending significantly more time flying and on the sea than females ($t = 3.45, P < 0.01$; $t = 2.52, P < 0.05$ respectively, Table 2). There was no sex difference in the amount of time spent diving or ashore, but mean dive duration of males was significantly longer than that for females.

EFFECT OF BROOD SIZE AND CHICK AGE

There was no significant difference in the mean number of foraging trips made per day by birds with one- and two-chick broods or between chicks aged 1–19 days or older (t tests, all $P > 0.10$, Table 3).

Total time away was, however, significantly greater for birds with broods of two than for birds with one chick ($F_{1,23} = 17.23$, $P < 0.001$, Table 3). Thus on average, birds with two chicks spent 1.68 hr longer each day diving compared with those with a single chick. This resulted in an average increase of 0.55 hr/day underwater and 0.26 hr/day potentially available for prey capture. The extra diving time was used to make an additional 11.7 dives/day ($F_{1,23} = 3.76, P = 0.07$). There was no difference in mean dive duration (F test, $P > 0.07$) or the proportion of diving time spent underwater (F test, $P > 0.5$) in relation to brood size.

There was no significant effect of chick age on any of the foraging activity variables. However, a decrease in time spent underwater by birds with broods in the second stage of the chick period approached significance ($F_{1,23} = 3.75$, $P = 0.07$, Table 3). Time allocated to flight, on the sea, or ashore showed no significant brood size or chick age differences.

TABLE 2. Characteristics of daily foraging activity (mean ± SD) for male and female South Georgian Shags during chick rearing. Data for birds making short dives have been excluded.

Activity variable	Females (n = 12)	Males (n = 12)
Trip frequency (trips/day)	2.5 ± 1.1	2.2 ± 0.6
Total time away (hr)	5.82 ± 1.36	6.79 ± 1.02
Time flying (hr)	0.28 ± 0.06	0.44 ± 0.16
Time on sea (hr)	0.14 ± 0.06	0.23 ± 0.10
Time ashore away from nest (hr)	0.18 ± 0.15	0.26 ± 0.30
Time diving (hr)	5.22 ± 1.40	5.86 ± 1.18
Time underwater (hr)	2.04 ± 0.57	2.13 ± 0.54
Percent time diving underwater	39.2 ± 4.8	36.2 ± 4.6
Estimated available prey capture time (hr)	0.97 ± 0.27	1.01 ± 0.26
Dive duration (sec)	196.3 ± 34.4	228.8 ± 36.3
Dive frequency (dives/day)	39.2 ± 16.9	35.2 ± 14.7

TABLE 3. Characteristics of daily foraging activity (mean ± SD) for South Georgian Shags with one- or two-chick broods in the first and second stages of the chick period. Data for birds making short dives have been excluded.

Activity variable	One-chick brood		Two-chick brood	
	Chicks aged:		Chicks aged:	
	1–19 days (n = 7)	20 or more days (n = 6)	1–19 days (n = 6)	20 or more days (n = 5)
Trip frequency (trips/day)	2.4 ± 0.3	2.7 ± 0.3	1.7 ± 0.3	2.6 ± 0.4
Total time away (hr)	5.90 ± 0.37	5.23 ± 0.40	7.57 ± 0.40	6.67 ± 0.44
Time flying (hr)	0.32 ± 0.04	0.31 ± 0.05	0.36 ± 0.04	0.46 ± 0.05
Time on sea (hr)	1.14 ± 0.18	1.02 ± 0.20	0.67 ± 0.20	1.05 ± 0.21
Time ashore away from nest (hr)	0.34 ± 0.09	0.22 ± 0.10	0.19 ± 0.10	0.11 ± 0.10
Time diving (hr)	4.98 ± 0.37	4.50 ± 0.40	6.83 ± 0.40	6.02 ± 0.44
Time underwater (hr)	1.88 ± 0.17	1.74 ± 0.18	2.65 ± 0.18	2.08 ± 0.20
Percent time diving underwater	38.0 ± 1.9	38.6 ± 2.0	38.6 ± 2.0	35.1 ± 2.2
Estimated available prey capture time (hr)	0.89 ± 0.08	0.83 ± 0.08	1.26 ± 0.08	0.99 ± 0.09
Dive duration (sec)	211.7 ± 15.4	219.7 ± 16.6	212.9 ± 16.6	204.8 ± 18.2
Dive frequency (dives/day)	34.1 ± 5.6	28.8 ± 6.0	48.7 ± 6.0	37.8 ± 6.6

DISCUSSION

South Georgian Shags on Bird Island exhibited the same sexually distinct activity patterns as did Antarctic Shags *P. bransfieldensis* on Anvers Island on the Antarctic Peninsula (Bernstein and Maxson 1984). However, in contrast to the situation on Anvers Island, we recorded exceptions to this rule. In one pair the male made the first feeding trip both on the days he and his mate were radio-tracked and on numerous occasions when we were present in the colony to check nest contents. In another pair the birds behaved as expected when they were radio-tracked but additional observations indicated that on some days the male fed first. For neither pair was there any obvious disadvantage in terms of breeding success as both reared chicks. At Anvers Island both day length and weather conditions influenced foraging patterns (Bernstein and Maxson 1984). In our study, female departure time, but not male return time, was significantly related to day length and there was no weather effect. The latter could have been due to the fact that maximum wind speeds experienced on Bird Island (10–15 m/sec G. Liddle, pers. comm.) were much less than those at Anvers Island (25–45 m/sec Bernstein and Maxson 1984).

Bernstein and Maxson (1984) speculated that the sexually distinct temporal patterns of feeding in Antarctic Shags might be associated with sex differences in foraging tactics, feeding habitats or diet. They concluded that a comparison of at-sea behavior of males and females might lead to a greater understanding of the adaptive pressures influencing feeding patterns. In our study, male South Georgian Shags spent significantly more time flying than females. Since they did not make more trips than females, this result implied that males had a greater foraging range and might, therefore, be exploiting a different feeding habitat. This interpretation was confounded by our observation that a considerable amount of a bird's flight time was spent repeatedly circling in front of the breeding colony, but it proved impossible to partition flight time of radio-tracked birds into circling and directional flight. Diving locations could not be determined with great accuracy but there was no evidence that the bearing or the strength of the radio signal while a bird was diving differed between the sexes, results which would have been apparent if feeding areas of males and females had been far apart. The seabed off Bird Island is extremely irregular and water depth can vary dramatically over short distances, so we cannot rule out the possibility that the two sexes were using different feeding habitats. Our results also indicated that mean dive durations of males were longer than those of females. For several other species of cormorant, dive duration has been shown to be correlated with water depth (e.g., Wilson and Wilson 1988, Trayler et al. 1989, Wanless and Harris 1991, Wanless et al. 1993). In South Georgian Shags, dive depth (or the depth of water where the bird is diving) also has a positive and significant effect on dive duration (Croxall et al. 1991, Kato et al. 1992, Wanless and Harris 1993), although Croxall et al. (1991)

concluded that within the shallow and deep dive categories, dive depth appeared to account for relatively little of the variation in dive time. Sex differences in dive duration might, therefore, be indicative of differences in foraging depths. However, to date dive depth data obtained using time-depth recorders have only been obtained from males. Because of their lower body mass, and hence smaller functional body oxygen store, females might be expected to exhibit a different dive-depth relationship to males (Cooper 1986). Clearly comparable data need to be obtained from females. Our data on at-sea activity did not therefore elucidate the reason(s) for the sexually distinct temporal patterns of feeding South Georgian Shags. The possibility remains that males and females take different sizes or species of prey, and further studies are needed to compare the diet of the two sexes.

On average, South Georgian Shags at Bird Island were away from the colony for 6.22 hr/day, ca. 30% less than Antarctic Shags rearing chicks at Anvers Island (overall mean 8.96 hr/day calculated from fig. 2 in Bernstein and Maxson 1985). Birds at the two colonies exhibited different responses to factors influencing activity budgets. Thus at Bird Island males tended to spend more time away than females and there was no evidence that time spent foraging increased with chick age (Tables 2 and 3). In contrast, at Anvers Island females allocated more time to foraging than males and both sexes spent more time away as their chicks got older. Brood size, the factor which had the greatest effect on total time away in our study, could not be investigated by Bernstein and Maxson because their results were obtained in a year of high chick mortality due to starvation and only single chick broods were present (N. P. Bernstein, pers. comm.). In contrast, breeding success in our study was 1.13 chicks/breeding pair ($n = 32$ nests) which appears to be an unusually high reproductive output for shags on Bird Island (J. P. Croxall and P. A. Prince, pers. comm.). Thus feeding conditions appeared to be very different in the two studies with data for South Georgian Shags collected during a good breeding season and those for Antarctic Shags collected in less favorable conditions. Clearly more information is needed for the two colonies to assess annual variation in activity budgets and reproductive output. In the only other study of foraging activity in a member of the Blue-eyed Shag group, Brothers (1985) recorded a mean trip length of 4.98 hr (range 2–7 hr) during chick rearing in the Macquarie Shag (*P. purpurascens*) at Macquarie Island. This was considerably longer than the 3.09 ± 1.02 hr recorded in our study. However, since the number of trips made per day by the Macquarie Shags was not quantified it is unclear whether the total time away/day was greater at Macquarie.

Detailed data on at-sea activity patterns of other Antarctic and subantarctic shag species are almost completely lacking. Results for Antarctic Shags on Anvers Island were based mainly on observations of color-banded birds which made it difficult to quantify behavior away from the breeding colony. Although dive durations (range 5 sec–3.5 min) there appeared broadly similar to those recorded in our study, activity patterns of birds away from the colony were radically different from those for Bird Island shags, with more than 90% of the time spent preening, resting or standing on shore and only 8.4% of time spent swimming or diving. While it is possible that the observational method used at Anvers Island overestimated the amount of time birds spent ashore, the difference was so pronounced that it is difficult to accept that this was the sole reason. Moreover, since chicks at Anvers Island were dying of starvation, it seems counter-intuitive that adults there should spend less, not more, time diving compared with shags on Bird Island where feeding conditions were apparently better. The proportion of at-sea time spent diving by South Georgian Shags was also substantially greater than that of European Shags *P. aristotelis* radio-tracked using identical methods to those used here, at a colony in southeast Scotland (Wanless and Harris 1992). These birds were absent, on average, for 5.12 hr/day and spent 49% of their time diving, 24% flying, 22% on the sea and 4% ashore away from the colony.

A striking feature of South Georgian Shag activity budgets was that although almost all the time away from the nest was spent diving, only a small proportion of this time was potentially available for prey capture. Thus on average, birds obtained their own daily food requirements and presumably approximately half those of their brood in about 1.06 hr. Because in most cases dive duration and recovery time on the surface were both long, diving rates were very slow, averaging 8.3 ± 5.8 dives/hr ($n = 26$). Such slow diving rate could potentially make individuals

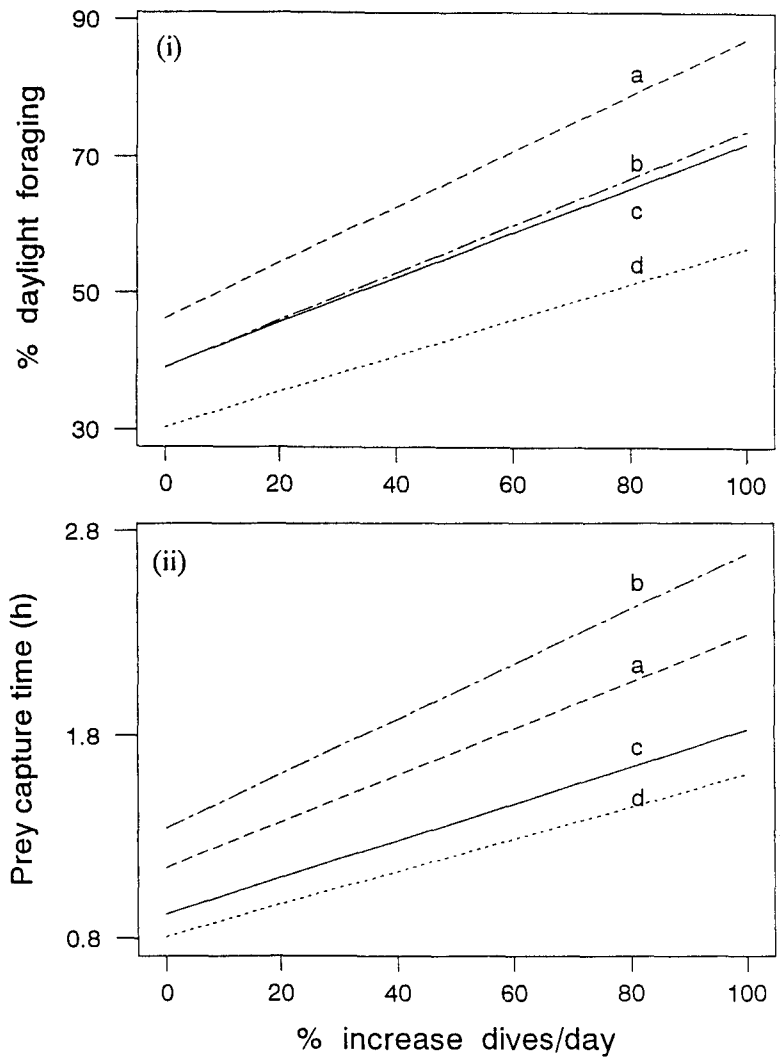

FIGURE 2. Predicted effects of a percentage increase in the number of dives/day on (i) the percentage daylight hours spent foraging, and (ii) the time potentially available for prey capture. Trends are shown for males with two-chick (a) and one-chick broods (c), and females with two-chick (b) and one-chick broods (d). Relationships for each category were calculated using the mean number of dives/day recorded in this study as a starting point.

sensitive to changes in food availability, since if prey capture rate decreases, a small compensatory increase in the number of dives has a relatively large effect on the time needed for foraging. We attempted to model this relationship by estimating what effect increasing the number of dives made in a day would have on shag activity budgets, assuming that other behaviors (e.g., dive parameters, time flying and on the sea, etc.) remained at the 1989–1990 values. For each bird we calculated how (1) the time used for prey capture, and (2) the percentage daylight spent away, increased as the number of dives made per day increased to twice that recorded in the study. Average values, estimated for males and females with broods of one and two young respectively, are shown in Figure 2. Since one member of the pair normally remains with the brood when the partner is away foraging, average total daily foraging times greater than 50% are unsustainable. The model indicates, that for pairs with broods of two, this threshold would be reached if the number of dives made per day increased by only 20% above the 1989–1990 levels, while dive fre-

quency could increase by 50% for pairs with single chicks (Fig. 2i). These limits indicate that birds have little capacity for increasing their foraging time and the maximum amount of time for prey capture is in the region of 1.1–1.6 hr/bird/day (Fig. 2ii). This suggests that the predominance of long, deep feeding dives by South Georgian Shags on Bird Island, imposes a severe limit on the time available for prey capture thus making the population very sensitive to changes in food availability.

ACKNOWLEDGMENTS

The senior author thanks the British Ecological Society for the provision of a Travel Grant to cover her air fare to the Falkland Islands. We are grateful to J. P. Croxall and P. A. Prince for help at all stages of the project, members of the British Antarctic Survey Bird Island base for assistance in the field, and N. P. Bernstein and an anonymous referee for helpful comments on an earlier version of the manuscript.

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