

# DIVING PATTERNS AND PERFORMANCE IN MALE AND FEMALE BLUE-EYED CORMORANTS

## *PHALACROCORAX ATRICEPS* AT SOUTH GEORGIA

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### SUMMARY

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The diving patterns of two male and one female Blue-eyed Cormorants *Phalacrocorax atriceps* were recorded with continuous-recording time-depth recorders for 10-13 days during the 1990 breeding season. For the female only data on time and depth were retrieved: diving was distributed through the day (including 31% at night); mean dive depth was 63 m. Males dived mainly in the afternoon and evening. Their mean dive depths were 61.4 and 83.9 m; mean dive durations 3.4 and 4.6 min; time at maximum depth (bottom time) averaged 28 and 44% of time submerged; descent time (0.4 and 0.5 min) was shorter than ascent time (1.6 and 2.9 min); dive/pause ratios were 0.4 and 0.5 and surface interval was not increased with preceding dive duration. The incubating male making one long dive bout per day, made fewer, longer dives, with less overall bottom time, than the chick-rearing male, which made at least two bouts per day. Most characteristics of diving in 1990 (a year of average breeding success) were similar to data from 1989 (a year of breeding failure). However, there were more, shorter dive bouts in 1989 and shallow (travelling) dives were more frequent: both consistent with lower prey availability in 1989 necessitating frequent changes of foraging sites.

### INTRODUCTION

Until recently cormorants were thought to forage in shallow water because they feed close inshore, chiefly on benthic fish, and to undertake relatively short (20-40 s) dives (Cooper 1986). However, recent direct measurements of diving performance have revealed that cormorants can dive much deeper than was previously thought (Burger 1991). Two male Blue-eyed Cormorants or Shags *Phalacrocorax*

*atriceps* at South Georgia regularly dived to 80-90 m on dives averaging 3-4 min in duration (Croxall *et al.* 1991). These results were sufficiently unexpected to warrant repeating the study, and to attempt to obtain data from female cormorants.

In this paper we report on the diving patterns and performance of two male and one female Blue-eyed Cormorant from the same colony at the same time of the year (but in the following year), using the same

dive recorders as Croxall *et al.* (1991). We compare the diving patterns of two males at different stages of the breeding cycle and compare the results with those from the previous study in relation to annual change in food availability, and examine how our results accord with models for air-breathing aquatic animals that feed on benthic prey (Kramer 1988, Wilson & Wilson 1988).

#### METHODS

The study was carried out at Bird Island, South Georgia (54S, 38W) in January 1990. The study site and field methods were as described in Croxall *et al.* (1991). The time-depth recorders (TDRs) were identical to those used previously, measuring 25 mm (diameter) by 85 mm (length) and weighing 73 g in air. The TDR consists of three main parts: a) recording paper and stylus; b) bellows-type pressure transducer; and c) quartz drive motor and gear shifts. It provides a continuous record of depth against time, from which dive depth, duration, time at or near maximum depth (bottom time), descent time, ascent time and surface interval between dives can be calculated (Croxall *et al.* 1991). TDRs were attached directly to the feathers of the central back using epoxy resin and removed 10-15 days later. The methods of processing the resulting data followed Croxall *et al.* (1991). Thus the basic unit of analysis was the daily diving period (time from first to last dive each day). Within this, discrete foraging bouts were delimited by taking disproportionately long (extended) surface intervals, identified using the method of surface-interval survivorship curves (Gentry & Kooyman 1986, Feldkamp *et al.* 1989), to define a bout-ending criterion (BEC) for each bird. If a surface interval between dives is longer than the BEC, each dive belongs to different bouts. Bouts were further defined as consisting of at least three dives.

TDRs (production numbers 31, 36, 42) were deployed on two male and one female cormorant on 14 January. The males were captured on 25 January (bird 42, weighing 2 375 g) and 28 January (bird 31, weighing 2 400 g) and the female on 24 January

(weighing 2 350 g). Male 31 was rearing three young chicks (hatched *c.* 6 January) which were still in good health on 15 February; male 42 was incubating three eggs, which remained unhatched by 15 February; female 36 had lost one of a brood of two chicks of very uneven size hatched before TDR attachment (*c.* 11-14 January), the remaining chick still being alive on 27 March.

Dive parameters between the two males and the relationship between dive parameters were examined for significant differences by Wilcoxon 2-sample tests and Spearman's coefficient of rank correlations, respectively.

#### RESULTS

The two recorders deployed on males worked perfectly and complete continuous data were obtained for 10 and 13 consecutive days (Fig. 1). With recorder 36, deployed on the female, however, the recording stylus did not advance smoothly during dives. Consequently, the only data that could be retrieved, from 11 days of recording, were the depth and timing of dives.

Timing and duration of foraging period and dive frequency

Both males foraged exclusively diurnally (Fig. 1), starting on average seven hours after sunrise (*c.* 0400) and continuing until late afternoon (male 42) or early evening (male 31), sunset being at *c.* 2000 (all times given as local time: GMT-2 h). The later finishing time of male 31 produced a significantly longer diving period with significantly more dives per day; however, the dive frequencies of the two males were similar, though significantly different (Table 1).

The female showed no consistent pattern in the timing of diving (Fig. 1) and 31% of dives were made between sunset and sunrise. The few dives (averaging 12 per day), spread through the day with long intervals between many of them, precluded calculation of foraging period and realistic dive

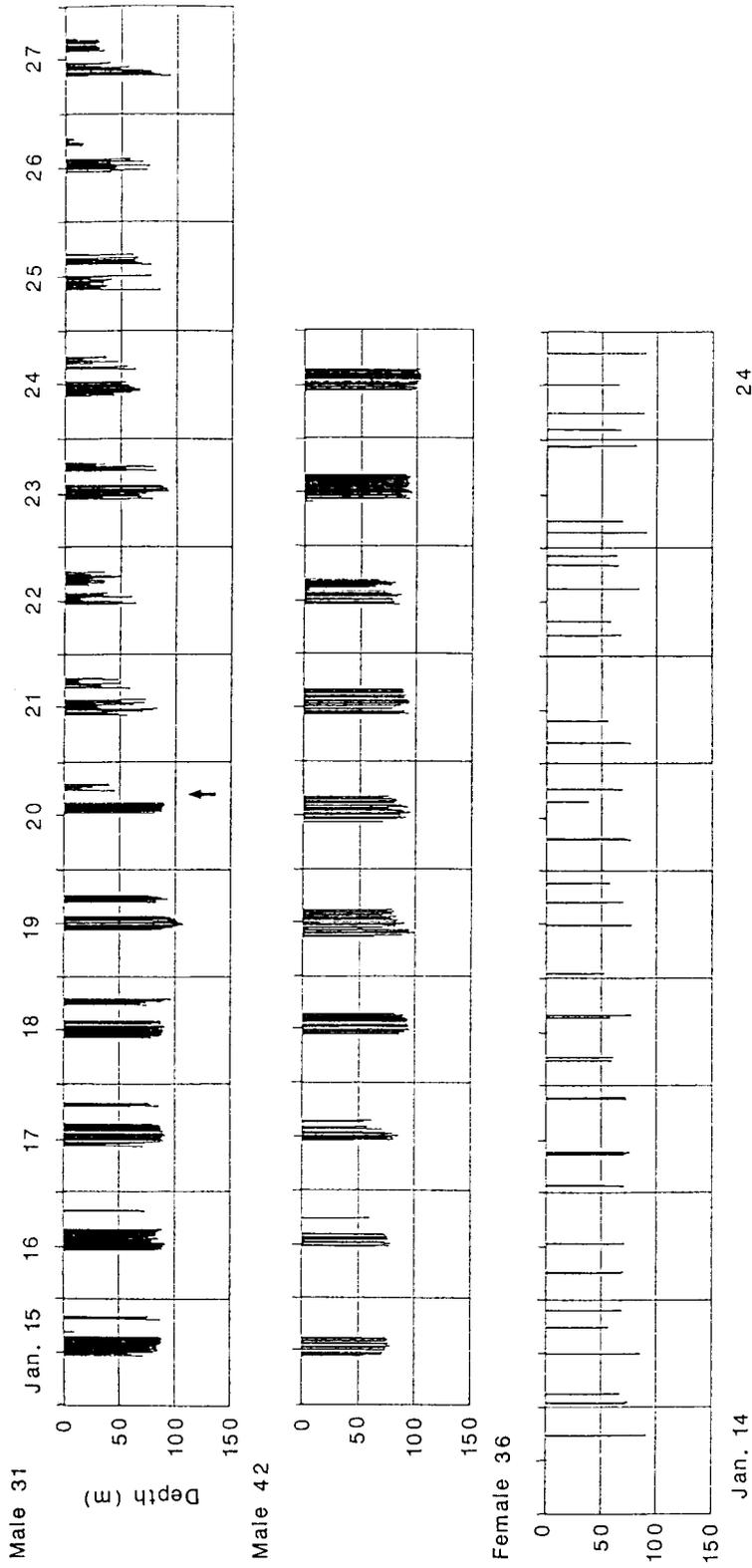


Figure 1

Diving record of Blue-eyed Cormorants . Each dive is shown as a vertical line. Arrow shows the transition point of diving pattern in male 31.

TABLE 1  
TIMING (LOCAL TIME) AND DURATION OF DIVING PERIOD AND NUMBER AND OVERALL FREQUENCY OF DIVES (DURING DIVING PERIOD) BY MALE BLUE-EYED CORMORANTS. VALUES ARE MEANS  $\pm$  S.D., WITH RANGES IN PARENTHESSES. SIGNIFICANT DIFFERENCES BETWEEN BIRDS INDICATED AS: \*  $P < 0.05$ , \*\*  $P < 0.01$ . OTHER DIFFERENCES N.S.

| Bird | n<br>(days) | Diving period                  |                                |                              | Dives                       |  |  |
|------|-------------|--------------------------------|--------------------------------|------------------------------|-----------------------------|--|--|
|      |             | Start                          | Finish**                       | Duration**<br>(h)            | Total**<br>per day          | Frequency*<br>(dives h <sup>-1</sup> ) |  |
| 31   | 13          | 1053 $\pm$ 62<br>(0848 - 1309) | 1917 $\pm$ 58<br>(1716 - 2039) | 8.4 $\pm$ 0.8<br>(6.6 - 9.8) | 28.7 $\pm$ 3.8<br>(21 - 36) | 3.4 $\pm$ 0.4<br>(3.1 - 4.6)           |  |
| 42   | 10          | 1100 $\pm$ 41<br>(0920 - 1150) | 1624 $\pm$ 48<br>(1534 - 1824) | 5.5 $\pm$ 0.7<br>(4.2 - 6.6) | 20.9 $\pm$ 4.0<br>(16 - 28) | 3.8 $\pm$ 0.6<br>(2.6 - 5.0)           |  |

frequency.

#### Dive depth, duration and transit and bottom times

Only eight dives (1%) lacked recognizable bottom time and these were generally shallower and shorter than the rest. The single such dive by male 31 was to 9.6 m and lasted 0.8 min. The seven such dives by male 42 were to  $16.0 \pm 18.1$  m (range 2.7–45.7 m) and lasted  $1.6 \pm 0.8$  min (range 0.7–2.8 min). Mean dive depth of the female bird was  $62.9 \pm 12.2$  m (range 24.2–91.0 m;  $n=134$ ), significantly shallower than male 42 ( $P<0.001$ ) and not significantly different from male 31 (Table 2). Dive depth of male 31 was significantly shallower and much more variable than male 42 (CV of 44% and 12% for males 31 and 42, respectively). Dive duration of male 31 was significantly shorter than that of male 42 (Table 2). After five consecutive days of consistent deep dives, male 31 made an abrupt transition on 20 January to more variable depth and comparatively shallow dives (Fig. 1); this behaviour persisted for the remaining seven days of the study. For male 31, mean dive depth in the first period was  $83.9 \pm 10.1$  m ( $n=165$ ), significantly deeper than in the second period ( $43.5 \pm 21.9$  m;  $n=208$ ) and not significantly different from male 42. Despite almost identical dive depths, male 42 made dives that lasted significantly longer than those of male 31 in the first period ( $3.8 \pm 0.4$  min).

Dive depth was significantly positively related to dive duration in males 31 and 42 ( $r_s=0.72$  and  $0.23$ , respectively) and inversely related to bottom time in males 31 and 42 ( $r_s=-0.28$  and  $-0.42$ , respectively,  $P<0.01$  for all) (Fig. 2).

Transit time (the sum of descent and ascent time) showed a similar pattern of variation to overall dive duration but bottom time was very similar for males (Table 2). Bottom time as a proportion of total time submerged on a dive therefore varied considerably, with males 42 and 31 spending 28 and 44%, respectively, at maximum depth. Although male 42 made fewer dives per day (Table 1), its longer dives

resulted in mean total daily time submerged being almost equivalent to that of male 31 (Table 3). Conversely, the mean total daily time spent at maximum depth of male 42 was significantly less than that of male 31.

#### Descent and ascent time

For both males descent times were significantly shorter (4–6 times) than ascent times. Descent time below the time resolution (0.3 min) of the TDRs was 44% and 39% of all dives for male 31 and 42, respectively. There were significant increases in ascent time with dive depth in males 31 and 42 ( $r_s=0.89$  and  $0.22$ , respectively,  $P<0.01$  for both) (Fig. 3). For male 31 increase in ascent time was proportional to dive depth. However, male 42 took longer to surface from any depth than did male 31 and disproportionately longer when diving shallower.

#### Dive bouts and organization of diving

The bout-ending criteria for males 31 and 42 were 14 and 19 min, respectively. This resulted in 99% of dives occurring within dive bouts of more than three dives. Characteristics of these bouts are summarized in Table 4. Male 42 showed only one dive bout on eight of 10 days with a significantly lower dive frequency, not significantly different but longer bouts and shorter daily total duration of bouts than male 31. Male 31 undertook at least two bouts on each day. For male 31 the mean interval between the first and second bouts in the first period (3.4 h) was significantly longer than in the second period (1.7 h) ( $P<0.01$ ). In the first period of male 31 the duration of the first bout ( $4.4 \pm 0.8$  h) was significantly longer than that of the second bout ( $1.2 \pm 0.5$  h) and dive depth was deeper in the first bout ( $86.3 \pm 4.8$  m) than in the second bout ( $76.0 \pm 5.7$  m) ( $n=5$ ;  $P<0.05$ ; Wilcoxon signed-ranks test). There was no significant difference in bout duration and in dive depth between the first and second bouts in the second period.

The relationships between dive duration (for dives

TABLE 2

NUMBER OF DIVES BY MALE BLUE-EYED CORMORANTS WITH (+BT) AND WITHOUT (-BT) BOTTOM TIME, DEPTH, OVERALL DURATION, TRANSIT, BOTTOM, DESCENT AND ASCENT TIME DURATION, FOR DIVES WITH BOTTOM TIME (+BT). VALUES ARE MEANS  $\pm$  S.D., WITH RANGES IN PARENTHESES. SIGNIFICANT DIFFERENCES BETWEEN BIRDS INDICATED AS: \*  $P < 0.05$ , \*\*  $P < 0.01$

| Bird | No. of dives |     | Depth**<br>(m)                    | Duration**<br>(min)          | Transit**<br>time<br>(min)   | Bottom time                  |                                  | Descent*<br>time<br>(min)    | Ascent**<br>time<br>(min)    |
|------|--------------|-----|-----------------------------------|------------------------------|------------------------------|------------------------------|----------------------------------|------------------------------|------------------------------|
|      | +BT          | -BT |                                   |                              |                              | (min)**                      | (%)**                            |                              |                              |
| 31   | 373          | 1   | 61.4 $\pm$ 26.8<br>(2.7 - 107.0)  | 3.4 $\pm$ 0.6<br>(2.0 - 5.0) | 1.9 $\pm$ 0.6<br>(0.2 - 3.5) | 1.5 $\pm$ 0.4<br>(0.5 - 2.9) | 44.4 $\pm$ 13.6<br>(15.4 - 91.9) | 0.4 $\pm$ 0.3<br>(0.0 - 1.8) | 1.6 $\pm$ 0.7<br>(0.4 - 3.5) |
| 42   | 202          | 7   | 82.8 $\pm$ 12.0<br>(38.1 - 103.7) | 4.6 $\pm$ 0.4<br>(3.1 - 6.1) | 3.3 $\pm$ 0.5<br>(2.1 - 4.7) | 1.3 $\pm$ 0.4<br>(0.5 - 2.3) | 28.2 $\pm$ 8.0<br>(9.1 - 47.8)   | 0.5 $\pm$ 0.4<br>(0.0 - 1.6) | 2.9 $\pm$ 0.4<br>(1.5 - 3.8) |

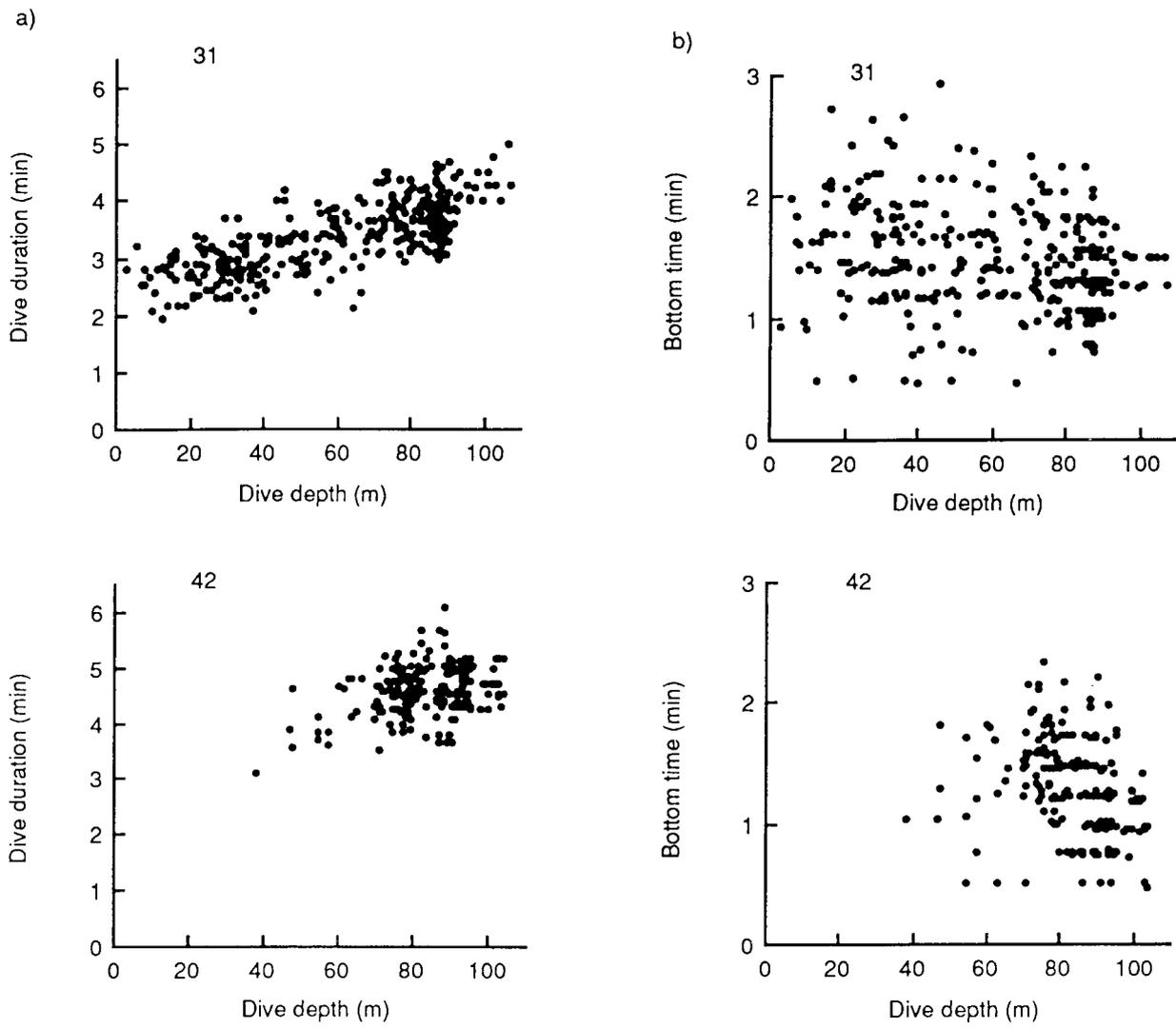


Figure 2

Relationships a) between dive depth and dive duration and b) between dive depth and bottom time for male Blue-eyed Cormorants.

TABLE 3

TOTAL DAILY TIME SUBMERGED AND AT MAXIMUM DEPTH (BOTTOM) OF MALE BLUE-EYED CORMORANTS. VALUES ARE MEAN  $\pm$  S.D., WITH RANGE IN PARENTHESES. SIGNIFICANT DIFFERENCES BETWEEN BIRDS INDICATED AS: \*\*  $P < 0.01$ . OTHER DIFFERENCE N.S.

| Bird | Time (min)                        |                                 |
|------|-----------------------------------|---------------------------------|
|      | Submerged                         | Bottom**                        |
| 31   | 97.9 $\pm$ 17.5<br>(74.0 - 133.6) | 42.4 $\pm$ 6.9<br>(34.7 - 56.1) |
| 42   | 93.8 $\pm$ 17.9<br>(72.2 - 117.6) | 26.2 $\pm$ 6.7<br>(12.7 - 34.6) |

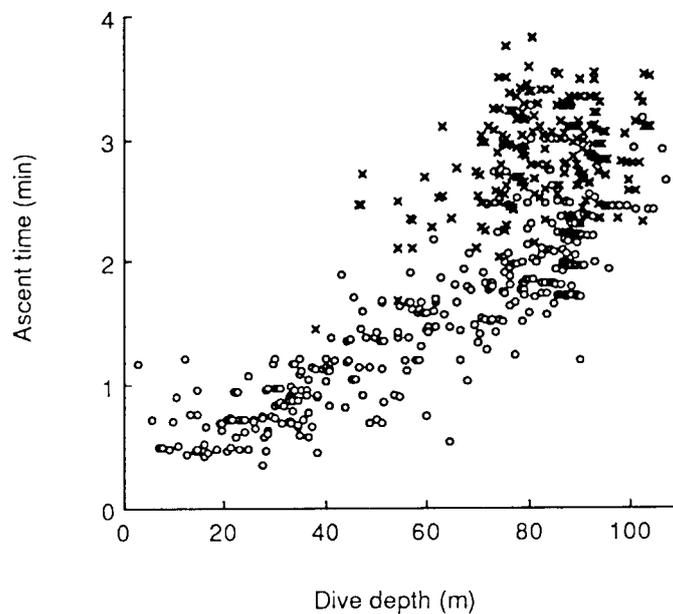


Figure 3

Relationships between dive depth and ascent time for chick-rearing (bird 31; circles) and incubating (bird 42; crosses) male Blue-eyed Cormorants.

TABLE 4

NUMBER AND DURATION OF BOUTS OF DIVING BY MALE BLUE-EYED CORMORANTS, AND NUMBER AND FREQUENCY OF DIVES IN BOUTS. VALUES ARE MEAN  $\pm$  S.D. WITH RANGE IN PARENTHESES. SIGNIFICANT DIFFERENCES BETWEEN BIRDS INDICATED AS: \*\*  $P < 0.01$ . OTHER DIFFERENCES N.S.

|  | 31                               | 42                               |
|--|----------------------------------|----------------------------------|
| No. of days  | 13                               | 10                               |
| No. of bouts per day**                               | 2.4 $\pm$ 0.9<br>(2 - 5)         | 1.4 $\pm$ 0.7<br>(1 - 3)         |
| Total duration of bouts<br>per day (h)               | 5.3 $\pm$ 0.6<br>(3.7 - 6.2)     | 4.9 $\pm$ 1.0<br>(3.4 - 6.3)     |
| % of daily diving period**<br>in bout                | 63.8 $\pm$ 6.1<br>(55.3 - 79.2)  | 90.2 $\pm$ 15.7<br>(52.3 - 100)  |
| Duration of bout (h)                                 | 2.2 $\pm$ 1.3<br>(0.4 - 5.1)     | 3.5 $\pm$ 2.2<br>(0.3 - 6.3)     |
| No. of dives per bout                                | 11.9 $\pm$ 6.8<br>(3 - 29)       | 14.8 $\pm$ 8.6<br>(3 - 28)       |
| Dive frequency in bout**<br>(dives h <sup>-1</sup> ) | 5.6 $\pm$ 0.8<br>(4.5 - 7.6)     | 5.0 $\pm$ 2.0<br>(3.6 - 10.8)    |
| Dive/pause ratio in bout                             | 0.41 $\pm$ 0.11<br>(0.25 - 0.69) | 0.53 $\pm$ 0.29<br>(0.32 - 1.49) |

with bottom time in bouts) and the subsequent surface interval are shown in Fig. 4. The relationships were significant but Spearman's correlation coefficients ( $r_s$ ) were only -0.21 and 0.15 for males 31 and 42, respectively.

Dive/pause ratios (Dewar 1924) were broadly similar for both birds (Table 4), surface times being 2-3 times the preceding dive duration. There was no tendency for dive/pause ratios or surface times to increase as diving progressed in the longer bouts.

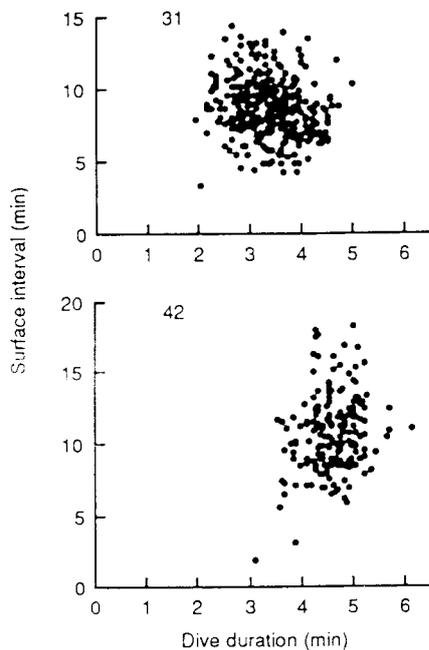


Figure 4

Relationships between dive duration and subsequent surface interval within dive bouts for male Blue-eyed Cormorants.

#### DISCUSSION

##### Comparison between sexes

Although diving depths were similar, there were substantial differences in the timing, pattern and frequency of diving between the female and male Blue-eyed Cormorants. Previously Bernstein &

Maxson (1984) showed that females foraged in the morning and remained at their nests in the afternoon, whereas males did the reverse. In the chick-rearing period at South Georgia, a few females showed much less regular activity patterns than did males and were recorded as being absent from the colony at sunset (S. Wanless & M.P. Harris unpubl. data). Despite the female undertaking only half as many dives per day as did the males, its chick was successfully brooded, suggesting that more reproductive effort is made by the male partner (cf. Bernstein & Maxson 1985). With data from only a single female the significance of these sex differences cannot be assessed. However, they suggest that there are large individual differences in the diving patterns of females.

##### Comparison between males

We have data from two males at different stages of the breeding cycle: incubating (bird 42) and chick-rearing (bird 31). The incubating bird usually undertook one bout per day (exchanging incubation duties with its partner on return), whereas the chick-rearing bird undertook at least two bouts, separated by an interval of 2-3 h. During this interval the chick-rearing bird returned to the colony and fed its chicks. The overall pattern, however, is consistent with male Blue-eyed Cormorants staying at the colony in the morning and foraging later in the day (Bernstein & Maxson 1984).

The incubating bird made fewer dives per day than did the chick-rearing bird. Likewise, despite similar dive depths, the incubating bird took longer to surface, indicating it travelled more slowly and/or at shallower angles. Both these results are consistent with incubating cormorants having considerably lower daily energy requirements than chick-rearing birds (Dunn 1975, Bernstein & Maxson 1985) and therefore needing to spend less time in the foraging area (at the bottom), permitting travel to be slower and/or less direct.

All studies (reviewed in Croxall *et al.* 1991) indicate that Blue-eyed Cormorants virtually exclusively take

benthic or benthic-demersal prey. If we assume that the dive depth reflects the depth of water then we can infer that the change in diving pattern in bird 31 coincided with a change in foraging site. In the first period the first bout always lasted longer with deeper dives than did the second bout, suggesting foraging in shallower water (perhaps closer to shore) in the second bout. In the second period shallow diving was characteristic of both bouts.

#### Comparison between years

Combining results for 1989 and 1990, we have data for male Blue-eyed Cormorants rearing one, two and three chicks (Croxall *et al.* 1991, this study) (Table 5). All three males were similar in having diving periods lasting 6-10 h a day and making deep long dives with substantial bottom time followed by surface intervals lasting 2-3 times the dive duration.

Fledging success in 1989 (0.1 chick per nest) was much lower than in 1990 (1.0 chick per nest). Poor reproductive success in 1989 suggested low food availability for Blue-eyed Cormorants. Differences in diving behaviour between the two years are consistent with this interpretation. Thus in 1989 there were more short dive bouts, suggesting that birds moved foraging sites more frequently. Also, 30% of the 1989 dives were shallow (<21 m) and lacked bottom time compared with 1% in 1990. Croxall *et al.* (1991) suggest that shallow dives are for travelling or possibly for exploiting prey visible from surface.

#### Descent time and ascent time

Descent times of Blue-eyed Cormorants are consistently shorter than ascent times, except for bird 33 in 1989, for which the times were similar. This suggests that cormorants swim faster in descent than in ascent or that they ascend at shallower angles than when descending. The TDR, however, cannot distinguish between these two possibilities. This pattern of shorter descent time and longer ascent time was affected neither by year nor breeding stage, which suggests that it has some structural,

physiological or behavioral basis. Descent and ascent rates, i.e. depth change per unit time, were 1.5-2.5 m.s<sup>-1</sup> and 0.6-2.2 m.s<sup>-1</sup>, for descent and ascent, respectively. These rates are similar to the mean swimming speeds of penguins (c. 2 m.s<sup>-1</sup>) (Wilson *et al.* 1989, Gales *et al.* 1990, Kooyman *et al.* 1992). Our results suggest that assumptions that wing- and flipper-propelled divers such as penguins and alcids can swim faster than foot-propelled divers like cormorants (Kooyman 1989) and that cormorants ascend vertically at the same velocity as they descend (Wilson & Wilson 1988) should be regarded with caution.

#### Models for air-breathing aquatic animals

Kramer (1988) suggested that optimal travel velocity would increase with depth. This was true for both male birds in our study. However, there were considerable differences between these birds. In particular the ascent rate of the chick-rearing Blue-eyed Cormorant was higher and more constant than that of the incubating bird, thereby minimizing travelling time. This might reflect that chick-rearing birds may have more severe time limitations for foraging and a higher energy requirement than incubating birds, because chick-rearing birds have to return to the colony more frequently to feed their chicks.

Wilson & Wilson (1988) suggested that air-breathing bottom-feeders would maximize bottom time with respect to dive and recovery times, that optimal bottom time would increase with depth and that the frequency distribution of bottom time would change with prey density, that is, the distribution would be normal and skewed to the left when prey density is low and high, respectively. However, in our study bottom time was inversely related to dive depth and mean bottom times from years with different prey availabilities were similar. Furthermore, the assumption of the Wilson & Wilson (1989) model, that recovery time is a function of dive time, does not accord with our results.

TABLE 5

## MEAN CHARACTERISTICS OF FORAGING PERIODS, DIVES AND DIVE BOUTS OF CHICK-REARING MALE BLUE-EYED CORMORANTS

| Year                                     | 1989      |          | 1990     |      |
|--|-----------|----------|----------|------|
| Bird                                     | 33F       | 33L      | 38       | 31   |
| Chicks                                   | 2         | 1        | 1        | 3    |
| Diving period                            |           |          |          |      |
| Start                                    | 0925      | 0955     | 1040     | 1053 |
| Finish                                   | 1955      | 1735     | 1700     | 1917 |
| Duration (h)                             | 10.5      | 7.7      | 6.2      | 8.4  |
| Dives <sup>-1</sup> /day                 | 68(38)    | 31(25)   | 29(20)   | 29   |
| Dive frequency <sup>1</sup><br>(dives/h) | 6.7(3.8)  | 4.0(3.2) | 4.6(3.2) | 3.4  |
| Dive parameters <sup>2</sup>             |           |          |          |      |
| Depth (m)                                | 78        | 83       | 94       | 61   |
| Duration (min)                           | 2.7       | 3.0      | 4.1      | 3.4  |
| Bottom time (min)                        | 1.5       | 1.9      | 1.3      | 1.5  |
| (%)                                      | 49        | 48       | 46       | 44   |
| Transit time (min)                       | 1.4       | 1.5      | 2.2      | 1.9  |
| Descent time (min)                       | 0.8       | 0.9      | 0.7      | 0.4  |
| Ascent time (min)                        | 0.6       | 0.7      | 1.6      | 1.6  |
| Bouts                                    |           |          |          |      |
| Bouts/day                                | 5         | 3.5      | 3        | 2.4  |
| Bout duration (h)                        | 1.3       | 1.1      | 1.5      | 2.2  |
| Dives/bout <sup>1</sup>                  | 14(8)     | 9(7)     | 10(7)    | 12   |
| Dive frequency <sup>1</sup><br>(dives/h) | 12.8(7.1) | 9.6(7.8) | 6.8(4.8) | 5.6  |

1. All dives, with deep dives in parentheses.
2. Deep dives only.

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