DIVING PATTERNS OF FULL-GROWN AND JUVENILE ROCK SHAGS¹

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Abstract. Information on diving patterns was obtained for full-grown and juvenile Rock Shags (*Phalacrocorax magellanicus*) feeding in Port Stanley Harbour, Falkland Islands. Birds dived mainly in, or just outside, beds of giant kelp within 50 m of the shore where the water depth varied from 1–6 m. Mean dive and recovery times were 28 sec and 10 sec respectively, diving rate was 1.8 dives/min and birds spent 75% of the time underwater. Full-grown and juvenile birds both showed a highly significant positive relationship between dive time and water depth. Full-grown individuals also showed a significant increase in recovery time with increasing dive time, but for juveniles recovery time was independent of dive time. This resulted in full grown birds attaining a rate of diving that was 30–50% higher than that of juveniles in shallow water.

Key words: Rock Shag; Phalacrocorax magellanicus; diving; dive-depth relationship; agerelated differences.

INTRODUCTION

Cormorants (Phalacrocoracidae) are foot-propelled pursuit-divers (Ashmole 1971) that typically alternate relatively short periods of active foraging fairly close to land with long periods of resting ashore or on water. This makes them convenient subjects for examining the relationships between various dive parameters and/or environmental variables, in particular water depth (e.g., Stonehouse 1967, Cooper 1986, Wilson and Wilson 1988). There appears to be no published data on diving patterns of Rock Shags *Phalacrocorax magellanicus* and this note presents data on dive and recovery times on the surface of fullgrown birds and juveniles of this species over a range of water depths.

METHODS

The study was carried out near a colony of at least 20 adult and ca. 50 immature-plumaged Rock Shags at Port Stanley Harbour, Falkland Islands between 23–25 November 1989 and 26– 28 February 1990. During the latter observation period ca. 20 recently fledged juveniles were also present indicating that breeding success (at ca. 2.0 young/pair) had been high. Although these juveniles were feeding themselves, some at least also received food from adults in the late evening when birds of all ages returned to the colony to roost.

All observations were made from the shores of the inlet in which Stanley Harbour is situated. To judge from birds seen leaving the colony and roosts, our viewing points covered most, and probably all, the feeding areas used by the birds from this colony. When a diving bird was located, a sample of ca. 10 (range 2-15) consecutive dives and recovery periods (the interval on the surface between successive dives) was timed to the nearest second with a stopwatch. For each of these dive series, we calculated the mean dive and recovery time, the diving rate (dives/min), and the percentage time underwater. Analyses involving percentages were performed using arc sin transformed data, but untransformed values are presented in the tables and text. Where possible, the angle at which the birds descended with respect to the surface (dive angle) was also recorded. The location of each bird was estimated by eye, using nearby features and the water depth at that point read off the Admiralty chart No. 2550 (Stanley Harbour) and corrected for the tidal height at the time of the observations. During November, 21 dive series were obtained from adults and eleven from immatures. For none of the dive parameters or depth relationships (see later) was there a significant difference between these two groups. The data were therefore combined (and birds termed full-grown) for comparisons with data collected from 19 series from

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| | | November | February | | | | | |
|----------------------|----|----------------------|----------|----------------------|----|------------------------------|----|------------------|
| | n | Full-grown x ± SD | n | Full-grown x ± SD | n | Juvenile $\hat{x} \pm SD$ | n | $\hat{x} \pm SD$ |
| Water depth (m) | 31 | 4.3 ± 2.3 | 19 | 4.9 ± 3.2 | 13 | 4.5 ± 1.9 | 63 | 4.5 ± 2.5 |
| Dive time (sec) | 32 | 29.8 ± 8.7 | 19 | 26.3 ± 10.7 | 13 | 27.4 ± 6.0 | 64 | 28.3 ± 8.9 |
| Recovery time (sec) | 32 | 9.5 ± 3.9 | 19 | 9.4 ± 4.6 | 13 | 11.5 ± 3.2 | 64 | 9.9 ± 4.0 |
| Dives/min | 30 | 1.7 ± 0.6 | 19 | 2.0 ± 1.3 | 13 | 1.6 ± 0.2 | 62 | 1.8 ± 0.8 |
| % of time underwater | 30 | 77 ± 5 | 19 | 73 ± 8 | 13 | 71 ± 17 | 61 | 75 ± 7 |

TABLE 1. Diving parameters of full-grown and juvenile Rock Shags.

birds in February, when both adults and immatures were in heavy wing and body molt, which made aging problematical.

Twelve pellets and five regurgitated fish were collected from two Rock Shag roosts during the February observation period.

RESULTS

Most dive series came from shags diving in, or just outside, beds of giant kelp (*Macrocystis* sp. and *Lessonia* sp.) within 50 m of the shore where the water depth varied from 1-6 m. Eleven series were from birds more than 100 m from the coast where the water was 7-13 m deep and where there was no obvious signs of kelp. Rock Shags mainly foraged solitarily except on a few occasions when two individuals dived within 20 m of each other.

We measured 64 series of dives. The mean depth of water where birds dived was 4.5 m; mean dive and recovery times were 28 sec and 10 sec respectively; the diving rate was 1.8 dives/ min, and birds spent 75% of the time underwater (Table 1). There were no significant differences between any of the categories of birds in water depth in the feeding area (ANOVA $F_{2,60} = 0.42$), dive time ($F_{2,61} = 0.97$) or recovery time ($F_{2,61} =$ 1.35). However, the proportion of time spent underwater (ANOVA $F_{2,58} = 3.52, P < 0.05$) was significantly lower for juveniles (71%) than fullgrown shags (77%) in November (t = 2.43, 41df, P < 0.05). Dives in water more than 7 m deep were invariably preceded by the bird leaping clear of the surface and an almost vertical angle of descent; in shallower water an individual usually slipped quietly under the surface and descended at ca. 45°.

In each category there was a highly significant positive linear relationship between dive time and water depth (Fig. 1, Table 2). The slopes of the regression lines did not differ but there was a significant difference between the intercepts of full-grown birds in November and February (t = 3.46, P < 0.001) which indicated that for any given depth, individuals spent less time underwater in February compared to November. This could imply differences in food availability in the two periods but we have no direct data to substantiate this. In both samples of full-grown birds there were significant increases in recovery time with increasing dive time (Fig. 2, Table 3). Neither the slopes nor the intercepts of these regression lines differed significantly. No relationship was apparent for juveniles for which recovery time appeared to be independent of dive time.

Taken together the relationships between dive time and depth, and recovery time and dive time, resulted in a significant decrease in diving rate with water depth (Fig. 3). However, slopes for the full-grown birds were significantly steeper than for the juveniles, such that in shallow water fullgrown individuals attained a rate of diving that was 30–50% higher than that of juveniles. For none of the three categories was there a significant linear relationship between the percentage of time underwater and either water depth or dive time.

In all of the dive series described above, Rock Shags were already diving when observations started and, except in two cases when individuals flew off, they continued to dive after observations ceased suggesting that birds were performing well in excess of 10 dives during a diving sequence. Three longer, but still incomplete, dive series were recorded from three birds in November that lasted 18.5, 25.3, and 30.5 min and contained 54, 40, and 60 dives respectively. None of the birds showed a progressive or marked decrease in dive time and/or increase in recovery time, patterns that would indicate that they were becoming exhausted.

We very rarely saw birds bring prey items to the surface and concluded that most prey must



FIGURE 1. Relationships between mean dive time and water depth for full-grown and juvenile Rock Shags diving in Port Stanley Harbour. Equations for the regression lines are given in Table 2.

have been swallowed underwater. The few items that we did see, and the contents of the regurgitated pellets, indicated that the Rock Shag's



FIGURE 3. Relationships between diving rate (y in dives/min) and water depth (x in m) for full-grown and juvenile Rock Shags. November full-grown n = 29, $r^2 = 0.53$, P < 0.001, y = 2.52 - 0.19x; February full-grown n = 18, $r^2 = 0.29$, P < 0.02, y = 3.11 - 0.22x; juveniles n = 11, $r^2 = 0.68$, P < 0.001, y = 2.11 - 0.12x.



FIGURE 2. Relationships between recovery time and dive time for full-grown and juvenile Rock Shags diving in Port Stanley Harbour. Equations for the regression lines for full-grown birds are given in Table 3.

main food was small fish. All 12 pellets contained fish otoliths (mean number/pellet = 61, SD = 46). Six also contained remains of crustacea, including three large isopods and four had 2–4 jaws from polychaete worms. All 12 contained grains of sand. The five intact fish that were collected had a mean length of 49 mm (SD = 8 mm) which agreed well with our visual estimates of the lengths of the few fish we saw held in birds' bills.

DISCUSSION

Our observations were in accord with those F. A. Cobb (In Murphy 1936) who reported that Rock Shags fed chiefly in kelp fields close to the coast. Cobb also noted that birds usually leaped almost out of the water before plunging beneath the surface; we mainly recorded this behavior in birds diving in water more than 7 m deep, in shallow water birds usually just slipped under the surface.

Cooper (1986) found a positive relationship

| | n | Regression equation | r ² | P |
|---------------------|----|---------------------|-----------------------|---------|
| November full-grown | 31 | T = 3.04D + 16.5 | 0.65 | < 0.001 |
| February full-grown | 19 | T = 2.79D + 12.6 | 0.68 | < 0.001 |
| February juvenile | 13 | T = 2.96D + 14.1 | 0.89 | < 0.001 |

TABLE 2. Relationships between dive time (T in sec) and water depth (D in m) for full-grown Rock Shags in November and February and juveniles in February.

between mean dive time and body weight among 18 other species of cormorant. There appear to be few published weights of Rock Shags but Humphrey et al. (1970) recorded values of 1,472 g and 1,386 g for two subadult females. Murphy (1936) found considerable overlap in bill and wing measurements of males and females which suggests that there may be little sexual difference in body size. Using Cooper's (1986) regression equation gives a predicted dive time of 23.8 sec for a 1,500 g cormorant, a value that is in general agreement with our observed values (Table 1).

However, to some extent mean dive time is not a very informative measure for this species because dive duration is strongly dependent on water depth. Positive dive-depth relationships have previously been demonstrated in at least seven species of cormorant (e.g., Dewar 1924, Stonehouse 1967, Wilson and Wilson 1988), and Wilson and Wilson (1988) argued that this indicated that birds were feeding on the bottom. We have no direct measure of where in the water column Rock Shags were foraging but the presence of sand in all the pellets suggests that most birds fed benthically on at least some of their dives. Wilson and Wilson also found that in Great Cormorant (P. carbo), Bank Cormorant (P. neglectus), Cape Cormorant (P. capensis), and Crowned Cormorant (P. coronatus) other dive parameters, e.g., bottom time, underwater swimming speed and distance traveled along the sea bed were all depth dependent but they did not report any increase in dive angle with water depth such as we observed. Increasing the dive angle reduces the time taken traveling between the surface and the feeding depth. Such behavior would be advantageous to birds diving in deeper water since it would increase the time potentially available for foraging.

Kramer (1988) suggested that in air-breathing species which feed underwater, recovery time would increase as a power curve function of dive time and some field data for cormorants support this (e.g., Stonehouse 1967; recalculated in Wilson and Wilson 1988, pers. obs.). However, in the Rock Shag the relationship appeared to be linear, at least over a range of dive times from ca. 5–50 sec. While percentage of time spent underwater was therefore independent of depth, diving rate decreased with depth (Fig. 3). Presumably some increase in prey profitability with increasing depth counteracts the reduced rate of diving in deeper water.

Age-related differences in foraging ability have been identified in other seabirds (e.g., Brown Pelicans (Pelecanus occidentalis) Orians 1969, Little Blue Herons (Egretta caerula) Recher and Recher 1969, Sandwich Terns (Sterna sandvicensis) Dunn 1972 and Adelie Penguins (Pygoscelis adeliae) Ainley and Schlatter 1972). Buckley and Buckley (1974) demonstrated that in the Royal Tern (S. maxima) only some aspects of foraging differed significantly between adults and juveniles which accords well with our results for the Rock Shag and those for the closely related Olivaceous Cormorant (P. olivaceous) (Morrison et al. 1978). In this latter study there was no difference in the diving abilities of adult and firstyear birds but prey capture efficiency was consistently lower in first-year individuals. Morrison et al. (1978) therefore concluded that immature

TABLE 3. Relationships between recovery time (R in sec) and dive time (T in sec) for full-grown Rock Shags in November and February and juveniles in February.

| | n | Regression equation | r ² | P |
|---------------------|----|---------------------|----------------|---------|
| November full-grown | 32 | R = 0.33T - 0.31 | 0.54 | < 0.001 |
| February full-grown | 19 | R = 0.28T - 2.02 | 0.42 | < 0.005 |
| February juvenile | 13 | - | 0.01 | > 0.1 |

foraging inefficiency was caused by a lack of subsurface abilities. We had no information on foraging success for the different age groups of Rock Shags but in this species there was a clear agerelated difference in the time on the surface between dives. Thus juveniles were apparently unable to recover rapidly after short dives which resulted in them having a slower diving rate in shallow water compared to full-grown birds. Immature Olivaceous Cormorants compensated for their reduced foraging success by spending more of the day feeding than adults (Morrison et al. 1978). Juvenile Rock Shags may also have adopted this strategy but some, and possibly all, were still being fed by adults (presumably their parents) at the breeding colony in the evenings. Therefore any shortfall in a juvenile's daily energy intake would to some extent be made up by parental feeding.

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LITERATURE CITED

- AINLEY, D. G., AND R. P. SCHLATTER. 1972. Chick raising ability in Adelic Penguins. Auk 89:559– 566.
- ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, p. 224–271. In D. S. Farner and

J. R. King [eds.], Avian Biology, Vol. 1. Academic Press, New York.

- BUCKLEY, F. G., AND P. A. BUCKLEY. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns (Aves: Laridae, Sterninae). Ecology 55:1053-1063.
- COOPER, J. 1986. Diving patterns of cormorants *Phalacrocoracidae*. Ibis 128:562–570.
- DEWAR, J. M. 1924. The bird as a diver. Witherby, London.
- DUNN, E. K. 1972. Effect of age on the fishing ability of Sandwich Terns (*Sterna sandvicensis*). Ibis 114: 360–366.
- HUMPHREY, P. S., D. BRIDGE, P. W. REYNOLDS, AND R. T. PETERSON. 1970. Birds of Isla Grande (*Tierra del Fuego*). Smithsonian Institution, Washington, p. 93.
- KRAMER, D. L. 1988. The behavioural ecology of air breathing by aquatic animals. Canad. J. Zool. 66: 89–94.
- MORRISON, M. L., R. D. SLACK, AND E. SHANLEY, JR. 1978. Age and foraging ability relationships of Olivaceous Cormorants. Wilson Bull. 90:414–422.
- MURPHY, R. C. 1936. Oceanic birds of South America. 2 vols. Macmillan Company, New York, p. 895–899.
- ORIANS, G. H. 1969. Age and hunting success of the Brown Pelican (*Pelecanus occidentalis*). Anim. Behav. 17:316-319.
- RECHER, H. F., AND J. A. RECHER. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons (*Florida caerulea*). Anim. Behav. 17:320–322.
- STONEHOUSE, B. 1967. Feeding behaviour and diving rhythms of some New Zealand Shags, Phalacrocoracidae. Ibis 109:600–605.
- WILSON, R. P., AND M.P.T. WILSON 1988. Foraging behaviour in four sympatric cormorants. J. Anim. Ecol. 57:943–955.