Diving depths of Shags *Phalacrocorax aristotelis* breeding on the Isle of May

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Information on maximum dive depth and the time spent at various depths was obtained from 49 Shags *Phalacrocorax aristotelis*. On average, the maximum dive depth was 33–35 m; the overall maximum was 43 m. Shags dived repeatedly to the same depth and spent *c.* 55% of the time between 25 and 34 m which indicated that they were foraging close to the seabed. About 46% of the time underwater was spent foraging and 54% travelling. Average underwater swimming speed was 1.7–1.9 m per second.

Shags and cormorants (Phalacrocoracidae) are foot-propelled pursuit-divers (Ashmole 1971). The marine species tend to feed within sight of land, at various levels in the water column, mainly in shallow (<5–8 m) water (Schreiber & Clapp 1987). However, to date there have been no direct measurements of the depths to which birds dive or where in the water column they feed (Cooper 1986). We used two types of miniature depth gauges to determine the proportion of time spent underwater at various depths and the maximum diving depth of Shags *Phalacrocorax aristotelis* breeding on the Isle of May, Firth of Forth, Scotland. In this paper we use these data on dive parameters in conjunction with information on bathymetry to deduce where in the water column Shags were feeding.

METHODS

Depth gauges

Fieldwork was carried out on the Isle of May (56°11'N, 02°33'W), between 20 June and 13 July 1989 at a colony of *c.* 1700 pairs of Shags. Fifty-seven birds were caught while they were rearing chicks. Each was sexed using the fact that males are vocal and females mute.

The maximum depth attained during a feeding trip was estimated using capillary-tube gauges made from 150 mm lengths of plastic tubing (internal diameter 1.6 mm) lined with a soluble indicator powder (Burger & Wilson 1988). Each gauge weighed *c.* 1.7 g (<0.1% of adult body-mass; mean mass of male Shags 1940 g, s.e. = 24, *n* = 4, mean mass of females 1598 g, s.e. = 22, *n* = 4) and was attached to a few feathers in the centre of the bird's back using a small cable tie (Plate 1). Forty-four maximum-depth gauges, deployed so as to cover the period when Shags were feeding (0400–2000 h GMT), were attached to birds under licence. Some devices, that were not recovered until 24 h after deployment, apparently gave spurious results since they indicated that birds had dived deeper than the water depth in the Shags'

feeding areas (see later). This was consistent with Burger & Wilson's (1988) finding that repeated submersions of a gauge to the same depth could lead to an over-estimate of the maximum depth. We attempted to minimize this potential error by recovering devices as soon as possible after a bird had been away diving. During chick rearing, birds on the Isle of May normally make 1–4 trips/day, each of *c.* 0.5–2.0 h duration (unpubl. data). We therefore imposed an arbitrary, but conservative, cut-off point and only analysed data from gauges that were recovered within 6 h of deployment. None of the devices in this category gave any indication of spurious results. After a gauge was recovered, the length of indicator remaining in the tube was measured to the nearest 0.5 mm and the equation.

$$d = 10.08\left(\frac{L_s}{L_d} - 1\right)$$

where L_s is the initial length (in mm) of undissolved indicator and L_d the length on recovery, was used to calculate the maximum depth (*d* in m) attained (Burger & Wilson 1988).

The total time spent at various depths during a feeding trip was estimated for 13 birds using a second type of gauge (90 mm long, and 11 mm in diameter) which weighed approximately 11 g (0.6% and 0.7% of the average body-mass of males and females, respectively). These time-at-depth gauges were attached to two or three central tail feathers with black waterproof tape (Wilson & Wilson 1989). They were deployed so as to cover the whole of the Shag feeding period and all were recovered 7–9 h after attachment. Each gauge consisted of a transparent cylinder enclosing a volume of air, bounded by a movable bung. Changes in hydrostatic pressure resulted in changes in the position of the bung in the cylinder which were recorded on photographic film by a light-emitting diode attached to the bung (Wilson *et al.* 1989). The film (Kodak Pan-X) was developed in Microdol-X. The cumulative time at each depth was estimated from the optical density of the image on the film, measured with a Schoeffel SD3000 spectro-densitometer, with the slit width set at 0.3 mm. The optical density was converted into a time estimate

Plate 1. Attachment of a maximum-depth gauge to a Shag.

for each 1 m depth-interval with reference to timed calibration exposures of the film (see Fig. 1). The error resulting from light spreading was reduced using a deconvolution procedure (Wilson *et al.* 1989), with the aid of a computer program developed by C. Noldeke (Institut für Meereskunde, Universität Kiel).

The calibration traces were made by lowering the gauges to predetermined depths in seawater for variable time periods (see Fig. 1). The internal lumens of our gauges were 81% longer than those in the prototypes described by Wilson *et al.* (1989), and were thus more sensitive to pressure changes and provided more precise depth estimates. Errors in estimating depths with these gauges were within 5% (pers. obs.), and errors in time estimates usually fall within 10% (Wilson *et al.* 1989). A constant, small amount of pressure is required to initiate movement of the bung (Wilson *et al.* 1989), which meant that times were recorded only for depths >2 m.

Diet

The diet of Shags during the period that the diving data were collected was estimated from 69 pellets regurgitated by adults. The contents of each pellet were examined under a binocular microscope and any fish otoliths identified to family or genus. The presence or absence of grains of sand was also recorded.
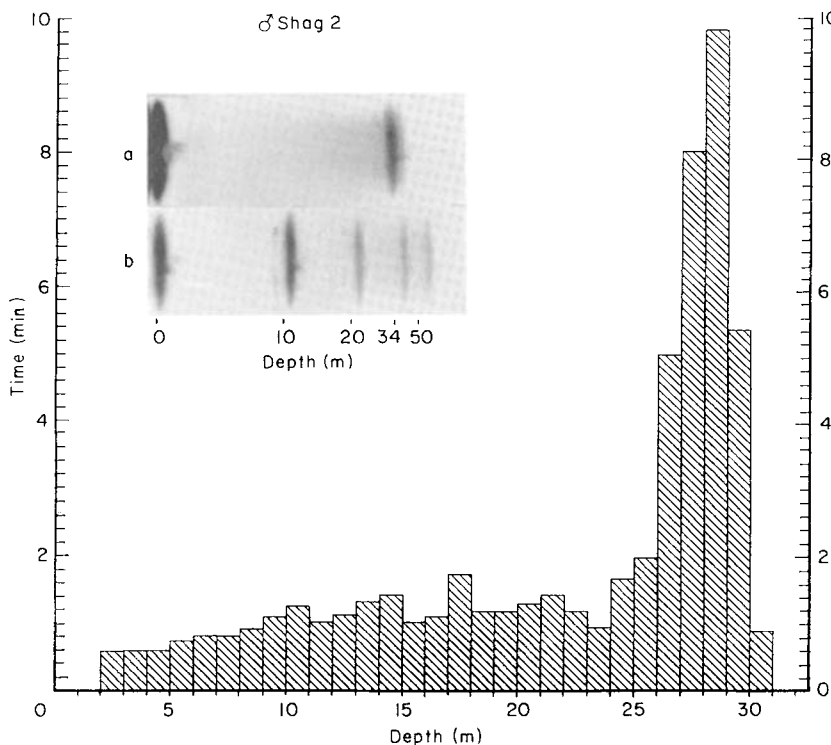

Figure 1. The time-at-depth histogram for one male Shag on the Isle of May. The insets show (a) the photographic trace obtained when the gauge was deployed on the bird, and (b) calibration traces when the gauge was suspended at depths of 10, 20, 34 and 50 m for periods of 15.0, 3.0, 1.0, and 0.67 min, respectively. The gauge did not record time at depths less than 2 m.

Table 1. *Mean maximum diving depths in metres of male and female Shags on the Isle of May using (a) maximum-depth gauges and (b) time-at-depth gauges*

	♂	♀	Total
(a) Maximum-depth gauges			
n	11	15	26
Mean ± s.e.	33 ± 2	34 ± 2	33 ± 1
Range	15–42	21–41	15–42
(b) Time-at-depth gauges			
n	7	6	13
mean ± s.e.	35.6 ± 1.4	35.5 ± 1.1	35.5 ± 0.9
Range	31–43	32–38	31–43

RESULTS

Maximum diving depth

Of the 44 maximum-depth gauges deployed, 26 were recovered successfully. They indicated that the mean maximum depth attained by male Shags was 33 m, which did not differ significantly from the 34 m recorded for females ($t = 0.20$, d.f. = 24; n.s.; Table 1). The absolute maximum depths recorded were 42 m and 41 m for males and females, respectively.

Time spent at depths

Time-at-depth gauges were successfully deployed on seven male and six female Shags. The photographic trace from one bird, a calibration trace and the resultant time-at-depth histogram are shown in Fig. 1. The bird showed a very characteristic dive pattern, diving repeatedly to the same depth. This result was typical of all birds, which spent, on average, 55% of the underwater time within the depth range 25–34 m (Fig. 2). The mean maximum depths obtained from the time-at-depth gauges did not differ significantly from those from the maximum-depth gauges (Table 1; males: $t_{16} = 1.1$, females: $t_{19} = 0.5$, both n.s.). The proportions of time spent at each depth did not differ between males and females (Fig. 2) (Kolmogorov–Smirnov test, $d_{max} = 0.112$, n.s.). All the birds appeared to move directly between the surface and the foraging depth, with the exception of one male that remained at 10–13 m for 11% of the underwater time, although it too spent the bulk of the time (53%) within the usual range (26–35 m).

If we assume for each bird that (a) the marked step in the time-at-depth histogram indicates the shallowest foraging depth, (b) the average underwater swimming speed is independent of depth and (c) birds did not feed while travelling down and up in the water, we can estimate the percentage underwater time spent foraging while allowing for the time taken to dive beyond the shallowest foraging depth. The mean (±s.d.) value was 43.2 ± 11.4 % (range
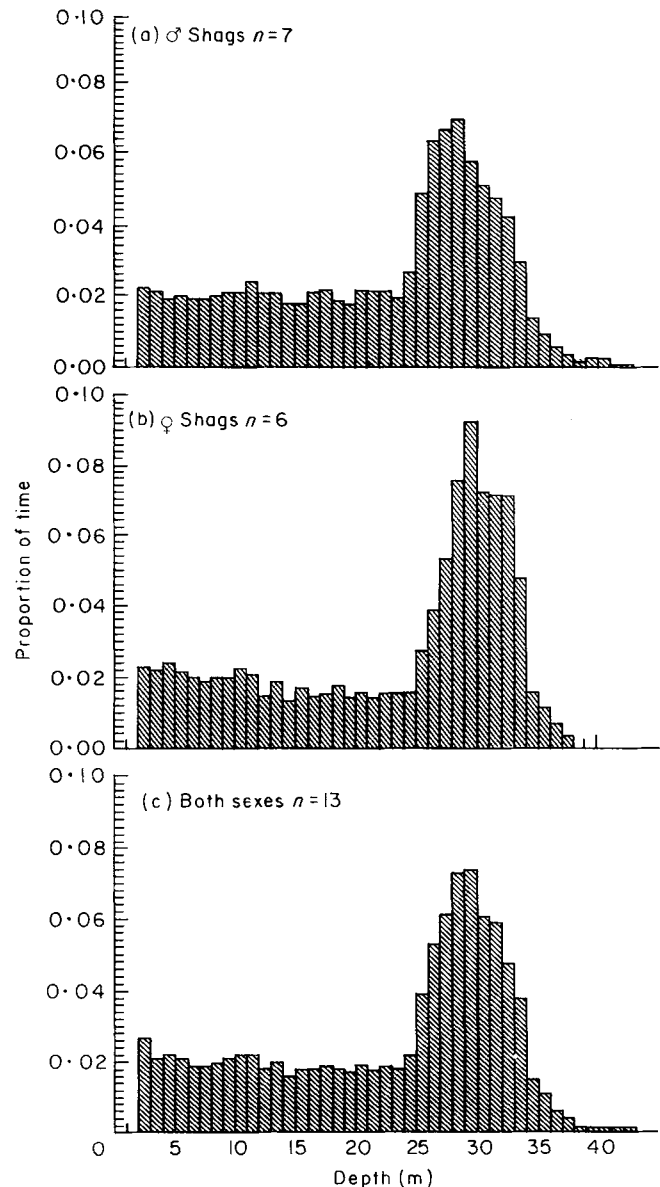

Figure 2. The mean proportion of underwater time spent in each 1 m depth category for: (a) seven males, (b) six females and (c) all 13 Shags combined. The gauges did not record time at depths less than 2 m.

19.8–62.2%, $n = 13$). The four lowest estimates (19.8–40.0%) came from two males and two females for which total underwater time was 10 minutes or less. All other birds had longer underwater times (16–166 minutes). With the four lowest estimates omitted, the mean percentage time in the foraging zone was 49.1 ± 6.8% (range 42.4–62.2%), with no significant difference between five males (mean = 45.7 ± 2.9%) and four females (mean = 53.3 ± 8.3%; two-tailed Mann–Whitney test, $U_{5,4} = 11$, n.s.). If the remaining underwater time is spent swimming down and up in the

Table 2. *Contents of 69 pellets regurgitated by adult Shags on the Isle of May*

Remains of prey	Sand present	Sand absent
Sandeel only	16	10
Sandeel and bottom-living fish	7	8
Bottom-living fish	1	3
No prey remains	6	18

water then, depending on the value for foraging used, Shags spent 51–57% of underwater time travelling.

Diet

Of 45 pellets regurgitated by adults that contained prey remains, 26 (58%) were composed entirely of sandeels *Ammodytes* spp., 15 (33%) also contained fragments of bottom-living species such as blenny (Cottidae), goby (Gobiidae) and flatfish (Pleuronectidae), and 4 (9%) contained just these other species (Table 2). Twenty-four (54%) of these pellets contained particles of sand as did 6 (25%) of the 24 pellets without prey remains.

DISCUSSION

Effect of instruments

Any recording device can potentially affect a bird's behaviour, and underwater the adverse effect appears to increase with the cross-sectional area of the instrument (Wilson *et al.* 1986). The cross-sectional area of the maximum-depth gauges used in this study was less than 10 mm², which is approximately 0.1% of the cross-sectional area of a Shag, and is, therefore, likely to cause minimal interference to diving behaviour. The fact that the estimates of maximum diving depth obtained from the larger time-at-depth gauges (cross-sectional area 95 mm², c. 1.0% of a bird's cross-sectional area), did not differ significantly from those from the capillary-tube gauges, makes us optimistic that they reflected accurately the utilization of different depths by these Shags. Our confidence is increased by the fact that we did not observe any obvious changes in attendance or parental behaviour in birds carrying either type of depth gauge.

Dive depth and pattern

The diving abilities of shags and cormorants have received much less attention than those of either penguins or auks (e.g. Kooyman *et al.* 1971, 1982, Adams & Brown 1983, Lishman & Croxall 1983, Montague 1985, Piatt & Nettleship 1985, Wilson 1985, Burger & Simpson 1986, Croxall *et al.* 1988). In addition to the data presented in this paper, we are aware of four other records of maximum diving depths, those

of 125 m for the Blue-eyed Shag *P. atriceps* (pers. obs.), 92 m for the Cape Cormorant *P. capensis*, 70 m for the Bank Cormorant *P. neglectus* and 11 m for the Crowned Cormorant *P. coronatus* (R. P. Wilson, pers. comm.). Although no cormorant has yet emulated the dives to over 200 m recorded by the Emperor Penguin *Aptenodytes forsteri* and King Penguin *A. patagonicus*, data from this study indicate that their diving ability, in terms of normal diving depths, is clearly on a par with many of the smaller penguins and auks (Piatt & Nettleship 1985, Kooyman 1989, Burger, in press).

The maximum depths we recorded greatly exceeded Dewar's (1924) figure of 6.4 m for Shags diving off the southeast coast of Scotland. However, this value was obtained by observing birds from the land and it is likely that no areas of deeper water were visible. In his review Dewar rejected records of birds drowned in fishing nets and therefore discounted Yarrell's (1845, quoted in Dewar 1924) observation of a Shag being taken from a crab-pot set at a depth of 37 m. However, information from drownings in nets is now considered to be more reliable (Piatt & Nettleship 1985) and to date the maximum depth recorded for the Shag comes from birds drowned in fishing nets set at 80 m in the Mediterranean (Guyot 1988).

Studies of both penguins and auks have demonstrated a positive relationship between maximum diving depth and body-mass (Piatt & Nettleship 1985, Prince & Harris 1988, Burger, in press). Given the marked sexual dimorphism exhibited by the Shag, with males being approximately 20% heavier than females, we might have expected to find a difference in maximum diving depth between the sexes, but no such effect was apparent. However, Guyot's (1988) results suggest that Isle of May Shags were diving well within the potential maximum depth for the species and it is therefore possible that any differences due to body-mass would not be apparent over the range of depths we recorded. Similarly Dewar (1924) could find no consistent evidence of sex differences in Shag diving behaviour in relatively shallow waters.

During the period that diving depths were being recorded we also collected data on the duration of 1172 dives made by seven other Shags, using radio-telemetry. The mean dive time for these birds was 74.2 s (s.e. = 3.5 s, n = 7 birds). Assuming that their diving patterns conformed to those of the individuals carrying depth gauges (which seems likely to be the case since the water depths where they were feeding were predominantly in the range 20–40 m), our estimates for the percentage of underwater time spent foraging (43–49%) and travelling (51–57%) suggest that, on average, Shags spent 32–36 s of a dive foraging and 38–42 s travelling down and up in the water column. Assuming that birds descend and ascend vertically to an average maximum depth of 35 m (Table 1), these figures indicate that Shags have an underwater swimming speed, while diving, of approximately 1.7–1.8 m per second. This is likely to be a minimum value since the Shag's angle of descent, although steep, is probably less than 90°. However, substituting a dive angle of 80° only increases the estimated underwater swimming speed to 1.7–

1.9 m per second. Previous estimates of the diving speeds of shags and cormorants have all been obtained from birds feeding in much shallower water than in this study. Thus Dewar (1924) estimated a minimum speed of c. 0.5 m per second from a single observation of a Shag bringing a bottom dwelling organism to the surface in c. 5 m of water, while Wilson & Wilson (1988) calculated speeds in the range of 0.80–1.24 m per second for Bank, Cape and Crowned Cormorants that were diving mainly in water less than 10 m deep.

Feeding depth

Data on diving depths provide information not only on a species' physiological ability to dive to particular depths but, when used in conjunction with knowledge of the bathymetry of the feeding area, can also indicate where in the water column a species normally feeds. Data from the radio-tracked birds and visual observations (both from the island and at sea) on where large numbers of untagged birds were feeding indicated that in 1989 Shags fed mainly in three distinct locations (Wanless et al. 1991). In all three areas the seabed was covered with coarse sand and the water depths were 18–30 m, 30–40 m and 35–40 m, respectively (I. Gatherum, pers. comm., pers. obs.). Assuming that the birds carrying depth gauges also fed in these areas, then the pattern of diving observed was consistent with individuals diving repeatedly to, or near, the seabed. Of the 39 birds followed only two (5%) provided any evidence of midwater feeding. Thus one male carrying a maximum-depth gauge dived to only 15 m, while another male with a time-at-depth gauge spent 11% of the time underwater at 10–13 m. However, these values could also be interpreted as birds diving benthically in shallower water.

Dewar (1924) also concluded that birds diving in water up to 6 m deep over a rocky bottom fed benthically but most information on where in the water column Shags feed has previously been derived from the species of prey taken. The diet of Shags in this study was broadly the same as that recorded in recent breeding seasons on the Isle of May (R. Forbes, pers. comm.) and at other British colonies (Steven 1933, Lumsden & Haddow 1946, Snow 1960, Mills 1969, Rae 1969). All these studies have found that sandeels form the bulk of the diet with species of Clupeidae, Gadidae and Cottidae occurring less frequently. Lumsden & Haddow (1946) concluded that although on occasions Shags must feed benthically in order to catch obligate bottom-dwelling fish (e.g. blennies, gobies, flatfish etc.), in general they foraged pelagically or semi-pelagically. This implies that they thought that Shags caught sandeels, which migrate vertically between the surface and the seabed (Macer 1966), in midwater. However, our data on dive patterns indicate that when birds were feeding predominantly on sandeels, they spent little time near the surface or in midwater but concentrated their effort on or near the seabed, which suggests that Shags may be more successful in catching sandeels at or near the sea-floor than in the water column.

Hobson (1986) found that the Pacific Sandlance A. hexapterus was vulnerable to predators when entering or leaving sandy refuges and predatory fish gathered on the bottom to attack fish moving into or out of the sand. The presence of particles of sand in the pellets further suggests that, at least on some occasions, Shags may take fish which are buried in the sand.

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