

USE OF TIME-AT-DEPTH RECORDERS FOR ESTIMATING DEPTH AND DIVING PERFORMANCE OF EUROPEAN SHAGS

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Abstract.—We used time-at-depth recorders and radio transmitters to measure dive parameters for European Shags (*Phalacrocorax aristotelis*). An algorithm for partitioning time-at-depth profiles, obtained from individuals making U-shaped, flat-bottomed dives, into foraging time and travel time is presented, and a Fortran program to run the algorithm is provided. The deepest dive recorded was 61 m, but foraging depth parameters varied considerably between colonies and years. On average, European shags spent 47.6% of their underwater time foraging. The duration of each stage of the dive cycle was a function of water depth. The observed trends were qualitatively similar to predictions of optimality models for air-breathing animals that feed underwater, but more data from individuals foraging at depths approaching the physiological maximum for the species are needed.

REGISTRADORES DEL USO DEL TIEMPO-A-PROFUNDIDAD PARA ESTIMAR UTILIZACION DE LAS PROFUNDIDADES Y RENDIMIENTO DE ZAMBULLIDA DE PHALACROCORAX ARISTOTELIS

Sinopsis—Utilizamos registradoras de tiempo a profundidades y radio-transmisores para medir los parámetros de zambullida de *Phalacrocorax aristotelis*. Se presenta un algoritmo para dividir los perfiles de tiempo en tiempo de búsqueda de alimentos y tiempo de viaje a diferentes profundidades, obtenido de los datos de individuos zambullendose en forma de U en fondos planos y un programa en FORTRAN para ejecutar el algoritmo. La zambullida más profunda registrada fue de 61 m, pero los parámetros de alimentación a diferentes profundidades variaron considerablemente entre diferentes colonias y años. *Phalacrocorax aristotelis* invirtieron un promedio de 47.6% de su tiempo bajo el agua buscando alimento. La duración de cada etapa del ciclo de zambullida estuvo en función de la profundidad del agua. Las tendencias observadas fueron cualitativamente similares a las predicciones de los modelos de optimización para animales de respiración aérea que se alimentan bajo el agua, pero se necesitan más datos de individuos buscando alimento a profundidades cercanas al máximo fisiológico para esta especie.

A wide range of diving birds (including penguins, auks, ducks, grebes, and cormorants) exhibit a positive relationship between dive duration and depth (e.g., Croll et al. 1992, Dewar 1924, Draulans 1982, Stonehouse 1967, Williams et al. 1992, Wilson and Wilson 1988, Ydenberg and Forbes 1988). For species such as cormorants, which feed benthically, this relationship is of particular interest because it suggests that water depth in

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the feeding area will be a major influence on the performance of birds exploiting it.

The European Shag (*Phalacrocorax aristotelis*) is a medium-sized (average body mass approximately 1750 g), pursuit-diver that feeds predominantly on small marine fish, particularly sandeels (*Ammodytes marinus*), which it catches on or just above the seabed (Harris and Wanless 1991, Lumsden and Haddow 1946, Snow 1960, Wanless et al. 1991). While visual observations have suggested that the species feeds mainly in shallow (<10 m) water (Dewar 1924), recent studies using depth gauges have shown that shags regularly dive to 40 m and show a time-at-depth profile that is characteristic of flat-bottomed diving (Barrett and Furness 1990, Wanless et al. 1991, Wilson et al. 1991). In this paper we present more extensive data on depth utilization by European Shags and describe a new method for partitioning time-at-depth profiles into time travelling through the water column and time spent foraging. Some birds fitted with time-at-depth recorders were also radio-tagged, and additional data on the durations of dives and recovery periods on the surface were available for these individuals. We were able to examine how durations of different stages of the dive cycle varied in relation to depth and to compare these results with predictions of models for air-breathing aquatic animals that feed on benthic prey (Houston and Carbone 1992, Kramer 1988).

METHODS

We conducted fieldwork on the Isle of May, southeast Scotland (56°11'N, 2°33'W), 20 Jun.–13 Jul. 1989 and 1–27 Jul. 1990, and at Sumburgh Head, Shetland Islands (59°51'N, 1°12'W), 17–21 Jul. 1990. Preliminary results from the Isle of May in 1989 have been published previously (Wanless et al. 1991), but the data were reanalyzed using the new algorithm (see below) to investigate the effects of sex, location, and year on diving parameters.

We obtained data on the use of different water depths by birds in the course of a feeding trip using time-at-depth recorders (Wilson et al. 1989). Breeding birds were caught at the nest using a thick wire hook attached to a 3-m-long bamboo pole. Each time-at-depth recorder weighed 11 g (about 0.6% of the mass of an adult European Shag) and was attached to two central tail feathers with black waterproof tape and small, plastic cable ties. All the depth recorders deployed were recovered successfully. Of the 27 deployments on the Isle of May, in 25 cases the time-at-depth recorders were recovered after the birds carrying them had made one feeding trip. The other two individuals had completed two, or possibly three, trips before they were recaptured. Four of the Shetland gauges were retrieved after a single trip, one bird was not recaptured until it had completed its seventh trip, and the number of feeding excursions made by one bird was not known precisely but was thought to be more than one. Birds were sexed using the fact that in this species males are vocal and females mute (Snow 1963).

A description of the construction and functioning of the depth record-

ers is given in Wilson et al. (1989). In brief, each device consisted of a transparent cylinder (approximately 90 mm in length and 11 mm in diameter) enclosing a volume of air bounded by a movable stopper. The position of the stopper varied in response to changes in hydrostatic pressure, and these movements were recorded on a small rectangle of photographic film by a light emitting diode attached to the stopper. The optical density of the image on the film was measured with a Schoeffel SD 3000 spectro-densitometer and converted into a time estimate for each 1-m depth interval using timed calibration exposures of the film. Calibration traces were made by lowering the gauges to pre-determined depths in seawater for variable time periods. The internal lumens of our gauges were 81% longer than those in the prototypes described by Wilson et al. (1989), making them more sensitive to pressure changes and consequently providing more precise depth estimates. Errors in estimating depths were within 5%, and errors in time were usually within 10%.

In 1990, seven birds on the Isle of May and five at Sumburgh Head were also fitted with radio transmitters. Each transmitter weighed about 19 g (combined depth recorder and transmitter load were less than 2% of body mass) and was attached to a few feathers in the center of the bird's back using waterproof tape and plastic cable ties. At both colonies signals from the tagged birds were monitored by an observer using an ATS R2100 scanning receiver. Changes in the characteristics and direction of the signal indicated when a bird was at the nest and when it was away feeding (Wanless and Harris 1992). Because signals in the 173 MHz band are not transmitted through seawater, dives were readily identified as breaks in transmission, and dive durations and recovery periods on the surface between dives could be timed to the nearest second. Mean dive durations and recovery durations were calculated for each individual. Eleven of the twelve birds carrying a transmitter and a time-at-depth recorder showed a uni-modal time-at-depth profile and relationships between various stages of the dive cycle and depth were examined by plotting mean dive and recovery durations of these birds against their mean foraging depth (see below). One individual with a multi-modal time-at-depth profile was excluded from the analysis.

Most traces showed broadly similar time-at-depth profiles with pronounced peaks at particular depths (Fig. 1), a pattern that is consistent with flat-bottomed rather than bounce dives (Wilson et al. 1991). Depths at which horizontal swimming occurs are likely to be those where the bird forages. In an attempt to examine how the total time spent underwater by a European Shag was divided between travelling through the water column and foraging time spent swimming horizontally we developed a more sophisticated version of the algorithm outlined in Wanless et al. (1991).

Full details of the algorithm are given as an Appendix but in brief the algorithm required the following input parameters: (1) the proportion of underwater time spent in each depth interval, (2) the vertical depth encompassed by the depth interval, (3) the maximum number of depth

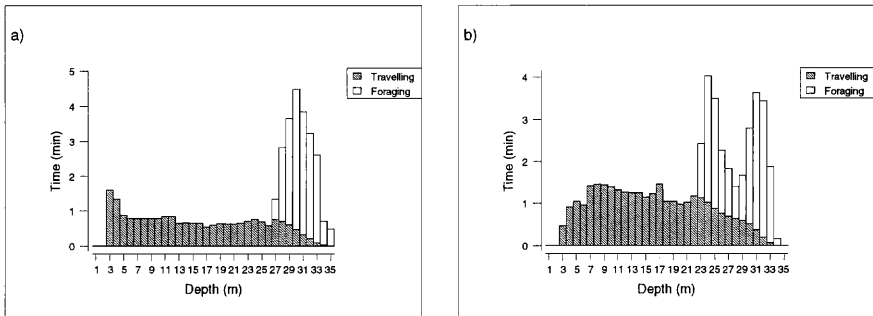


FIGURE 1. Examples of unimodal (a) and multimodal (b) time-at-depth profiles of European Shags.

intervals, (4) the number of depth intervals near the surface for which data are unreliable, (5) the numbers of depth intervals between the surface and the shallowest foraging depth, and (6) the mean dive time for the recorded sequence (if available). The algorithm does not estimate the number of depth intervals between the surface and the shallowest foraging depth (m_f). Instead, it requires that the user provide an estimate of the depth over which no foraging occurs. This reflects the difficulty of writing a general and objective algorithm that can be guaranteed to provide sensible estimates. For the results of this paper, the driver program generated a first guess for parameter m_f and plotted a histogram, with the selected point shown. The user could then choose that value or substitute another. Similarly, the user could change the specified value for the number of depth intervals near the surface for which data are unreliable. From this information four output parameters were estimated: (1) the percentage of underwater time spent foraging, (2) the proportion of time at each depth interval spent foraging, (3) the proportion of total foraging time spent foraging at each depth interval and (4) the average vertical speed while travelling (in those cases where a mean dive time was available).

For each bird we estimated four foraging depth variables: (1) the minimum foraging depth, (2) the maximum foraging depth, (3) foraging depth range (i.e., the difference between the maximum and minimum values) and (4) the mean foraging depth (Fd_{mean}) which was estimated as:

$$Fd_{\text{mean}} = \sum_i (P_i) (i)$$

where P_i is the proportion of total foraging time spent foraging at each depth interval i . One depth interval corresponded to one meter and so the units of Fd_{mean} are meters.

The effects of sex, year, or colony site on foraging depth parameters and the relationship between the duration of different stages of the dive cycle and mean foraging depth were investigated using General Linear Models (GLM, Minitab 1993) in which mean values for each individual

TABLE 1. Mean \pm SD (range) foraging depth parameters and % time underwater spent foraging by European Shags on the Isle of May in 1989 and 1990 and Sumburgh Head 1990.

	Isle of May				Sumburgh Head		Total	
	1989		1990		1990			
	(n = 13)		(n = 14)		(n = 6)		(n = 33)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Minimum foraging depth (m)	23.2	8.2	15.1	5.3	23.0	16.6	19.8	9.8
	(6-31)		(4-27)		(4-44)		(4-44)	
Mean foraging depth (m)	30.1	2.0	19.7	4.6	32.2	13.4	26.1	8.3
	(27.1-34.0)		(14.0-30.6)		(12.4-51.2)		(12.4-51.2)	
Maximum foraging depth (m)	35.6	3.2	25.7	8.0	40.8	14.4	32.4	10.0
	(31-43)		(16-45)		(24-61)		(16-61)	
Depth range (m)	12.4	10.2	10.6	9.9	17.8	16.3	12.6	11.3
	(5-37)		(3-41)		(5-49)		(3-49)	
% time underwater foraging	44.7	9.7	48.5	13.1	51.6	8.0	47.6	11.0
	(27.3-62.4)		(29.5-67.8)		(40.6-62.4)		(27.2-67.8)	

were analyzed as independent responses. Previous analyses of the relationships between the durations of various stages of the dive cycle and depth have found evidence of non-linearity (e.g., Ydenberg and Guillemette 1991). Therefore, we fitted data for the European Shag using linear and quadratic regression and selected the model giving the best fit.

RESULTS

A total of 33 usable traces was obtained, 13 and 14 from the Isle of May in 1989 and 1990, respectively, and 6 from Sumburgh Head in 1990. The total amount of underwater time recorded for each individual varied from 5.7-454.9 min (median = 41.7 min, interquartile range = 23.3-84.0 min, $n = 33$).

Twenty-nine (88%) time-at-depth profiles were uni-modal, indicating that the bird had dived repeatedly to the same depth (Fig. 1a). The remaining four traces were multi-modal (Fig. 1b). In general, these were cases where the individual had made several trips suggesting that birds had used several different feeding areas over a relatively short period of time.

Applying the algorithm to the time-at-depth data to partition underwater time between travel and foraging indicated that shags foraged over a wide range of depths. At both colonies the minimum recorded foraging depth was about 5 m. The maximum depth attained by birds from the Isle of May was about 45 m; the maximum at Sumburgh Head was 61 m (Table 1). On the Isle of May, year had a significant effect on minimum ($F_{1,23} = 9.62$, $P < 0.01$), mean ($F_{1,23} = 59.35$, $P < 0.001$), and maximum ($F_{1,23} = 18.25$, $P < 0.001$) foraging depths with birds feeding at shallower depths in 1990 than 1989. There were no significant sex effects, nor were any of the interactions between year and sex significant on the Isle of

May. Foraging depth range was not significantly influenced by year or sex on the Isle of May. Only one male was sampled at Sumburgh Head so it was not possible to test for sex effects at this colony. Minimum, mean, and maximum foraging depths were all deeper at Sumburgh Head compared with the Isle of May in 1990 but only the difference in maximum depth was statistically significant (*t*-test; $P = 0.05$). There were no significant differences in minimum, mean or maximum foraging depths between Sumburgh Head and the Isle of May in 1989 (*t*-tests; all $P > 0.42$) nor for foraging range in either year (*t*-tests; both $P > 0.35$).

On average, a bird spent $47.6 \pm 11.0\%$ ($n = 33$) of its underwater time foraging (Table 1). There were no significant year or sex effects in percentage foraging time for individuals on the Isle of May (year: $F_{1,23} = 0.63$, $P = 0.4$; sex: $F_{1,23} = 0.0$, $P = 1.0$; year \times sex: $F_{1,23} = 0.06$, $P = 0.8$). There were no significant differences between Sumburgh Head and the Isle of May in the percentage time foraging in either year (*t*-tests; both $P > 0.13$).

The number of dive cycles recorded for the radio-tagged individuals varied from 18 to 96 with a mean of 42.1 ± 24.5 , ($n = 11$ birds). Mean dive duration was dependent on mean foraging depth; there were no significant differences in slope or intercepts between colonies or sexes (depth: $F_{1,4} = 24.62$, $P < 0.01$; sex: $F_{1,4} = 0.30$, $P = 0.6$; colony: $F_{1,4} = 2.31$, $P = 0.2$; depth \times sex: $F_{1,4} = 0.54$, $P = 0.5$; depth \times colony: $F_{1,4} = 2.14$, $P = 0.2$). The relationship was best described by a linear regression (Fig. 2a). Mean surface duration also increased significantly with depth, and there was a significant difference in slopes between the sexes (depth: $F_{1,4} = 87.13$, $P < 0.001$; sex: $F_{1,4} = 5.8$, $P = 0.07$; colony: $F_{1,4} = 0.0$, $P = 1.0$; depth \times sex: $F_{1,4} = 11.12$, $P < 0.05$; depth \times colony: $F_{1,4} = 0.08$, $P = 0.8$). In a quadratic regression the quadratic term was significant ($P < 0.02$) but the linear term was not ($P = 0.2$). The linear term was therefore dropped to give the relationship shown in Fig. 2b. However, the evidence for non-linearity was strongly influenced by the bird with a mean foraging depth of 41.6 m. After excluding this record there was no evidence of non-linearity over the depth range 12–30 m.

The relationships between depth and dive times and surface times were used to calculate dive and surface durations for those individuals for which only depth data were available (samples where the time-at-depth profile was multi-modal were excluded). Average foraging time per dive for each bird was calculated from the estimated mean dive time multiplied by the proportion of underwater time spent foraging, and travel time was given by dive time minus foraging time. Durations of both foraging time ($F_{1,23} = 17.72$, $P < 0.001$) and travel time ($F_{1,23} = 46.99$, $P < 0.001$) were dependent on mean foraging depth; there were no significant sex or colony differences in slope or intercept. The relationships were best fitted by a linear regression (Fig. 2c,d). Diving efficiency (the proportion of the dive cycle spent foraging) was related negatively to depth ($F_{1,23} = 15.93$, $P < 0.001$) and there were no significant sex or colony differences in slope or intercept. The relationship was best described by linear regression (Fig. 2e).

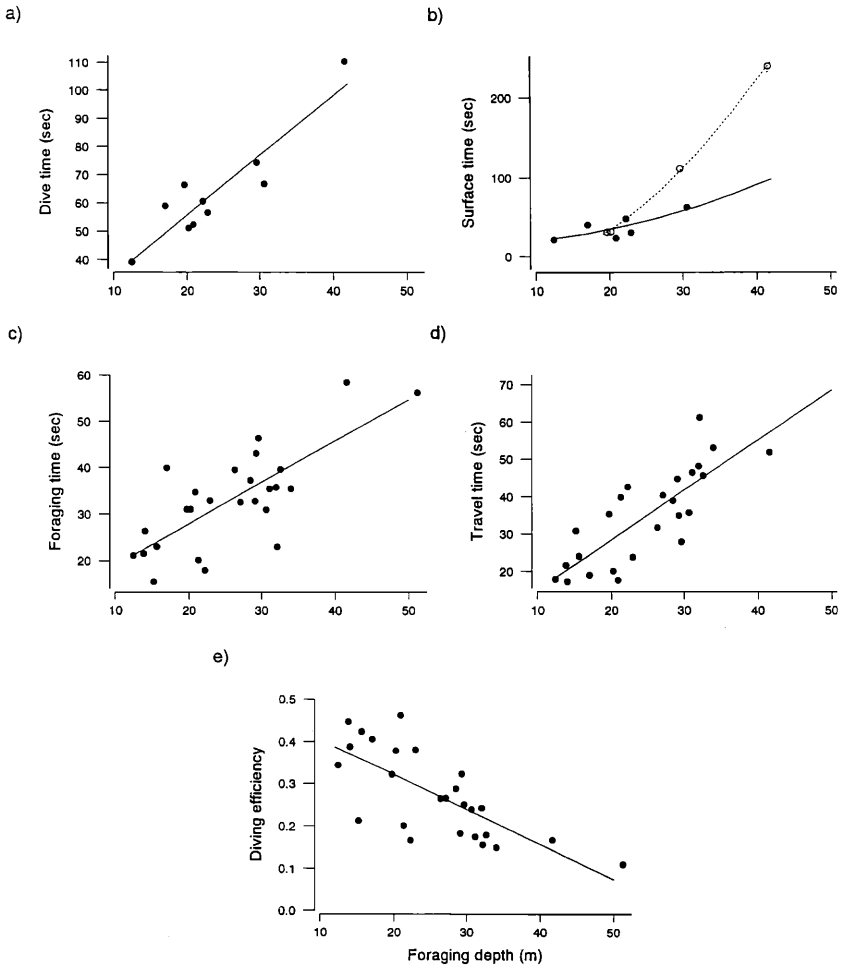


FIGURE 2. (a) Dive time, (b) surface time, (c) foraging time, (d) travel time, and (e) diving efficiency in relation to mean foraging depth (Fd_{mean}) for European Shags. Regressions for the lines are: a) dive time = $2.12 Fd_{mean} + 13.2$; $r^2 = 84.3\%$, $P < 0.001$; b) males (solid symbols and line), surface time = $0.05 Fd_{mean}^2 + 15.1$, $r^2 = 61.3\%$, $P = 0.06$; females (open symbols, broken line), surface time = $0.16 Fd_{mean}^2 - 30.8$, $r^2 = 99.9\%$, $P < 0.001$; c) foraging time = $0.89 Fd_{mean} + 10.2$, $r^2 = 57.0\%$, $P < 0.001$; d) travel time = $1.34 Fd_{mean} + 1.61$, $r^2 = 73.2\%$, $P < 0.001$; e) diving efficiency = $0.49 - 0.083 Fd_{mean}$, $r^2 = 52.6\%$, $P < 0.001$.

DISCUSSION

Three different types of depth recorder are currently in use in studies of diving behavior of marine birds. The simplest is the maximum-depth recorder, which is basically a sealed length of narrow gauge plastic tubing lined with a soluble indicator powder (Burger and Wilson 1988). Such

devices are inexpensive and, after recovery, information on maximum dive depth can be determined using a simple formula. Maximum-depth recorders are ideal for: (1) collecting preliminary data for a species, (2) use on small species where a heavy or bulky recorder might have an adverse effect, and (3) cases where the probability of recapture of an individual is low (Chastel 1994, Harris *et al.* 1990, Prince and Jones 1992, Wanless *et al.* 1988, Weimerskirch and Sagar 1996, Wilson *et al.* 1986). Their main disadvantage is that they provide information about only one aspect of diving performance, namely the maximum depth attained.

The time-at-depth recorders described in this paper were developed to quantify not only the range of depths used, but also the amount of time spent in each depth band (Wilson *et al.* 1989). Like maximum-depth recorders they are inexpensive, easy to construct, and easy to deploy in the field. Accessing information on depth utilization can only be achieved after the traces have been scanned using a spectro-densitometer. However, such instruments are standard equipment in many university laboratories. Because of their small size and mass (about 11 g), time-at-depth recorders are particularly useful for studies of alcids (e.g., Burger and Powell 1990, Burger *et al.* 1993, Croll *et al.* 1992), which may be affected by the attachment of devices (Wanless *et al.* 1988).

Although estimating the amount of underwater time spent in each depth band is relatively straightforward, assessing how an individual partitions this time between foraging and travel is more complicated. The algorithm (and Fortran Program to run it) presented in the appendix provides an effective method for partitioning underwater time between these activities in species that make flat-bottomed dives and greatly enhances the value of data collected using such devices. However, despite these improvements, information from time-at-depth recorders is inevitably limited compared to the wealth of data that can be collected using mechanical or electronic time-depth recorders (TDRs) in which individual dive profiles are recorded (Croxall *et al.* 1991, Watanuki *et al.* 1996). To our knowledge, only one study so far has compared the performance of time-at-depth recorders and TDRs, and in this case the two types of device produced similar results (Croll *et al.* 1992). Currently, the main disadvantages of TDRs are (1) their high cost and (2) their relatively large size and mass which makes them less suitable either for studying small species or those where the probability of successful recapture is low. However, smaller, more hydrodynamically shaped devices are being developed and these will ultimately be the first choice in most modern studies of diving animals.

This study confirmed that dive depth in European Shags is markedly greater than suggested by visual observations (Dewar 1924). The maximum depth of 61 m attained by a bird at Sumburgh Head is the deepest dive so far measured and suggests that the record of a bird drowned in a fishing net set at 80 m in the Mediterranean (Guyot 1988) accurately reflects the diving ability of this species. However, more data from instrumented birds, particularly at colonies surrounded by deep water where

birds are potentially able to approach their physiological limit, are needed.

Compared with other similar size *Phalacrocorax* species that have been studied using depth recorders, the maximum foraging depth of European Shags appears to be less than that of Blue-eyed Shags (*P. atriceps*) (107–116 m, Croxall et al. 1991, Kato et al. 1992), but slightly greater than Japanese Cormorants (*P. capillatus*) (45 m, Watanuki et al. 1996). The relationship between durations of different stages of the dive cycle and dive depth were broadly similar in European Shags and Japanese Cormorants with dive time, bottom time, travel time and surface time all increasing as a function of dive depth (Watanuki et al. 1996, this study). In contrast, in the Blue-eyed Shag diving depths were strongly bimodal. Although the durations of different stages of the dive differed markedly between deep and shallow dives, within each type depth explained rather little of the variation in dive parameters (Croxall et al. 1991). Studies of several other species of cormorant feeding in relatively shallow water (<10 m deep), and based on visual observations, have also found significant relationships between water depth at the feeding location and different stages of the dive (e.g., Trayler et al. 1989, Wanless and Harris 1991, Wilson and Wilson 1988).

Our results also indicate that European Shags exhibit considerable flexibility in foraging depth with mean values for individuals varying between years at the same colony and between colonies. Visual and telemetry data suggested that this variation was due to birds using different feeding areas and continuing to feed benthically, rather than individuals switching between benthic, midwater, and surface feeding in the same area. Thus, most of the instrumented birds followed on the Isle of May in 1989 apparently fed close to the colony in an area where the water was 30–40 m deep, whereas in 1990 the main feeding area was near the mainland where the water depth varied from 15–30 m (pers. observ.). Similarly at Sumburgh Head shallow dives were known to have been made close inshore where the water was less than 10 m deep, while foraging depths of the other individuals were all broadly consistent with the water depth in the feeding area. However, Grémillet et al. (in press) found that European Shags at a colony in Normandy, France did make some pelagic dives, which suggests that the species exhibits considerable flexibility in its foraging techniques.

Several interspecific comparisons of marine birds have shown that maximum dive depth is a function of body size (e.g., Burger 1991, Wilson 1991). Many cormorant species are sexually dimorphic with males larger and heavier than females (Johnsgard 1993). Thus differences in dive parameters between the sexes might be expected. In both Japanese Cormorants and King Cormorants (*P. albiventer*), species in which the average mass difference between males and females is 26% and 19% respectively, dive depth and duration were indeed significantly greater in males than females (Kato et al. 1996, Watanuki et al. 1996). In contrast, among European Shags on the Isle of May (where the mass difference between

sexes was approximately 20%) we found no evidence of a significant sex effect in dive depth or duration. The only significant difference between males and females that we recorded was the relationship between surface duration and depth in which surface time increased more rapidly in females (Fig. 2b). While the sample sizes used to determine these relationships were small, we previously showed that males required a shorter recovery period after long dives compared with females (Wanless *et al.* 1993), a result that is consistent with the findings of the present study.

For air-breathing animals that forage by diving, the ability to search for food is limited by the oxygen-storage capacity of their body tissues. One option for a diver would be to keep dive time constant. Under this rule dive duration would be independent of depth, but foraging time would decline linearly. However, numerous studies, including this one, have provided no evidence for this strategy but have instead found a positive relationship between dive duration and depth. Building on the work of Kramer (1988), Houston and Carbone (1992) developed marginal value models predicting how such divers should allocate their feeding time in order to maximize the rate of energy intake. In general, our results were qualitatively consistent with the model predictions in a number of respects. The optimality models predict that time at the surface between dives should increase roughly in proportion to depth over most of the depth range but accelerate rapidly near the maximum depth for the species. In the European Shag, the relationship over the range 12–30 m was linear with a doubling of dive time resulting in surface time increasing by 1.6 times (Fig. 2a, b). With the inclusion of data from the only individual making deeper dives, the relationship became significantly non-linear, suggesting that surface times were disproportionately longer on deeper dives. Although further data, particularly from birds foraging near the maximum depth (presumed to be at least 80 m) are needed, additional support for a non-linear response comes from a previous study of radio-tagged European Shags in which water depth at the feeding area was used as an index of dive depth (Wanless *et al.* 1993).

A novel prediction of the Houston and Carbone (1992) optimality models is that foraging time first increases and then decreases with water depth. However, over the depth range sampled in our study, the relationship was linear with foraging time increasing on average by 0.9 s for every meter increase in foraging depth. Once again more data from deep-diving birds are needed to investigate the relationship further.

As expected, travel time and foraging depth were positively related, with travel time increasing, on average, by 1.3 s for every additional meter of depth, indicating an average vertical travel speed of approximately 1.5 m/s. However, the observations from the deepest diving birds suggested that the relationship might be non-linear with travel speed being greater on deeper dives. Observations of several species of cormorant indicate that dive angle may vary and that in some cases the angle becomes steeper as dive depth increases (Wilson and Wilson 1988). This effectively means that travel time is proportionately shorter on deep dives although swim-

ming speed per se does not vary. Such a strategy is adopted by penguins (Wilson 1995) but no data for European Shags are currently available.

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APPENDIX. Algorithm for analyzing dive time by depth data.

A Fortran program to run the algorithm can be accessed from the directory /user/ftp/put/steve through anonymous ftp by typing

```
ftp dolphin.dcs.st-and.ac.uk
```

When prompted for a login name type 'anonymous' and when prompted for a password type in your e-mail address. This automatically takes you into /user/ftp and you can change directory to 'pub/steve' by typing in 'cd pub/steve'. You can then use the 'get' command to copy the file 'TRAVEL' onto your machine.

The ftp directory can also be accessed over the World Wide Web with the URL

```
ftp://www-ruwpa.dcs.st-and.ac.uk/
```

The following is a list of input parameters to algorithm TRAVEL.

- P_i = proportion of dive time spent in depth interval i
- w = depth interval width (1 m for the shag data)
- m_{max} = maximum number of depth intervals
- m_{min} = number of depth intervals near the surface for which data are unreliable
- m_f = the number of depth intervals between the surface and the shallowest foraging depth
- \bar{t} = mean dive time for the recorded sequence (if available)

The algorithm estimates the following output parameters.

- π = percentage of dive time spent foraging
- q_i = proportion of time in depth interval i that was spent foraging
- r_i = proportion of total foraging time that is spent foraging in depth interval i
- s_v = mean vertical speed while travelling

It also calculates

- m_g = greatest depth interval for which data were recorded ($m_g \leq m_{max}$)

The algorithm does not estimate the parameter m_f . Instead, it requires that the user provides an estimate of the depth over which no foraging occurs. This reflects the difficulty in writing a general and objective algorithm that can be guaranteed to provide sensible estimates. For the results of this paper, the driver program generated a first guess for parameter m_f and plotted a histogram, with the selected point shown. The user could then choose that value or substitute another. Similarly, the user could change the specified value for m_{min} if the histogram suggested the choice was poor.

The output parameters from TRAVEL are estimated as follows. Calculate

$$\bar{p}_i = \left\{ \sum_{i=m_{\min}+1}^{m_f} p_i \right\} / (m_f - m_{\min}),$$

so that \bar{p}_i is the average time at each depth interval, expressed as a proportion of total dive time, for intervals $m_{\min} + 1, \dots, m_f$.

Next assign $p_i = \bar{p}_i$, $i = 1, \dots, m_{\min}$, and evaluate

$$p_s = \sum_{i=1}^{m_g} p_i$$

Thus p_s is a scaling factor, as the p_i with the addition of the first m_{\min} values, will no longer sum to one.

Suppose estimates \hat{q}_i are available. Define

$$\hat{b}_i = \frac{p_i \cdot \hat{q}_i}{\sum_{j=1}^{m_g} p_j \cdot \hat{q}_j} \quad (1)$$

Thus \hat{b}_i is an estimate of the proportion of foraging time in depth interval i or deeper that is spent in depth interval i .

Let

$$\hat{c}_i = \begin{cases} \bar{p}_i, & i = m_f + 1 \\ \bar{p}_i \cdot \prod_{j=m_f+1}^{i-1} (1 - \hat{b}_j), & m_f - 2 \leq i \leq m_g \end{cases} \quad (2)$$

Thus, for each increment in i , \hat{c}_i is discounted by multiplying by the proportion of foraging time in depth interval i or greater that occurred at depth greater than i . For any foraging in depth interval i , the associated average vertical travel within that depth interval will be half the interval width, so that the multiplicative factor to account for interval i itself is $(1 - \hat{b}_i/2)$. Hence the proportion of time in interval i that is spent foraging is estimated by

$$\hat{q}_i = 1 - \frac{\hat{c}_i \cdot (1 - \hat{b}_i/2)}{p_i} \quad (3)$$

However, we need estimates \hat{q}_i in order to calculate the \hat{b}_i . Estimation may be carried out iteratively as follows. First set

$$\hat{q}_i = \begin{cases} 0.0, & 1 \leq i \leq m_f \\ 1.0, & m_f < i \leq m_g \end{cases}$$

Now for each i in turn, starting at $i = m_f + 1$ and finishing at $i = m_g$, perform the following steps.

Evaluate \hat{b}_i and \hat{c}_i from equations (1) and (2) respectively. Substitute \hat{b}_i and \hat{c}_i into equation (3); if $\hat{q}_i < 0$, set $\hat{q}_i = 0$. Proceed to the next value of i .

Now calculate

$$\hat{f}_s = \sum_{i=m_f+1}^{m_g} p_i \cdot \hat{q}_i$$

The percentage of dive time spent foraging is then estimated by $\hat{\pi} = 100 \cdot \hat{f}_s / P_s$

The above steps for $i = m_f + 1, \dots, m_g$ are now repeated. This process continues until $\hat{\pi}$ converges.

The average dive depth is estimated by

$$\bar{d} = w \cdot \left(m_f + \frac{\sum_{i=m_f+1}^{m_g} \hat{u}_i}{\bar{u}_f} \right)$$

where

$$\hat{u}_i = \frac{p_i \cdot (1 - \hat{q}_i)}{p_s}$$

estimates u_i = proportion of total dive time that is spent travelling in depth interval i , and

$$\bar{u}_f = \frac{\sum_{j=1}^{m_f} \hat{u}_j}{m_f}$$

Then

$$\hat{r}_i = \frac{100 \cdot p_i \cdot \hat{q}_i}{p_s \cdot \hat{\pi}}$$

and the average vertical speed of travel is estimated by

$$\hat{s}_v = \frac{2 \cdot \bar{d}}{\bar{t} \cdot (1 - \hat{\pi}/100)}$$

Thus the numerator is twice the estimated mean dive depth (because the bird must travel down then up), and the denominator is an estimate of the mean travelling time per dive.