

SURFACE BEHAVIOURS OF FEEDING SHAGS OFF LUNDY

By

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SUMMARY

Shags off Lundy were observed while engaged in prolonged bouts of diving for food, and their behaviour during the surface intervals between dives was recorded. Behaviours having a specifiable direction (Facing, Looking, Diving and Taking off at the end of a bout of dives) were found to show directional selectivity: Shags rarely dived in the direction away from land, and never took off towards land. They tended to face in the direction of diving, but to look in other directions. These patterns of behaviour are consistent with the birds using landmarks on shore to maintain their position during a bout of dives. Non-directional behaviours (including shaking, lifting and dropping the head, shaking tail or feathers, spreading and flapping wings, bill dipping, feather washing, preening and circling) were all more frequent in surface intervals terminated by take-off than in surface intervals terminated by diving, and for some of the behaviours (eg. Head Shake, Wing Flap, and Wash Feathers) the difference was very large and significant. These behaviours could therefore serve as social signals for intended flight.

INTRODUCTION

Shags (*Phalacrocorax aristotelis*), like a number of other birds, feed by diving under water to catch their prey, which in the case of Shags consists mainly of bottom-dwelling fish such as Sand Eels (Lumsden and Haddow 1946). Since the original observations collected by Dewar (1924), there has been substantial research on birds' diving behaviour, and in particular the behaviour of Shags (eg. Wanless, Burger and Harris 1991; Wanless *et al* 1993a; Wanless *et al* 1993b; Lea, Daley, Boddington & Morison 1996).

Most of this recent research has concentrated on the problems a diver faces in feeding efficiently. An air-breathing animal that feeds under water faces a conflict between two goals. The speed with which it can re-oxygenate its lungs will determine what proportion of its time, during a feeding bout, it can spend under water, and optimality arguments imply that this proportion should be as high as possible. Time spent on the surface is thus treated as time essentially lost from the feeding process because of the inconvenient necessity to breathe.

However, casual observation of diving birds suggests that a number of behaviours are characteristic of the surface periods during diving bouts. This paper therefore aims to shift the focus, by looking at time spent on the surface as interesting in its own right, rather than just as a necessary interruption to time spent under water. We pose the question of what diving birds actually do on the surface during their feeding bouts, other than breathing, and what functions those behaviours might have.

Optimality considerations in fact lead to some predictions of the functions surface behaviours might have. Although it is clear that an optimally diving animal should spend as much total time as possible under water, it leaves open the question of how that time should be distributed, that is, how long it should spend under water on each dive. Dewar (1924) showed that for birds, diving efficiency (measured as time under water divided by time on the surface) was relatively characteristic of species and genera, but the mean dive time varied substantially according to circumstances such as

the depth of water, with longer mean dives in deeper water. Kramer (1988) showed how this pattern could be predicted from a simple optimality model which took into account two principles:

- (a) time spent travelling from the surface to feeding depth, and back again, is time wasted; on this basis, each dive (and hence each surface time) should be as long as possible;
- (b) re-oxygenation of the lungs and blood at the surfaces is subject to diminishing returns as the concentration of oxygen in the blood increases; on this basis, each surface time (and hence each dive) should be as short as possible.

Kramer showed that the optimal compromise between these two contradictory principles would be struck at a longer mean dive when the animal is feeding at greater depth.

Lea *et al* (1996) argued from Kramer's analysis that an optimal diver would have to anticipate when it was going to make a longer dive, and stay longer on the surface before such dives to prepare for them, rather than staying longer on the surface after them in order to recover. Reporting data from four species of cormorants and Shags (*Phalacrocorax*), they showed that only the Shag (*P. aristotelis*) showed exclusively anticipatory breathing as predicted on the basis of Kramer's model, though the Cormorant (*P. carbo*) and the Pied Shag (*P. varius*) showed evidence of anticipatory breathing combined with reactive breathing. This concept of anticipatory breathing suggests a function for behaviour while on the surface. If an animal is to anticipate a long dive, it must in some sense know how long it is going to dive for before it does so. There are a number of sources of such knowledge. For example, the bird may be able to remember how densely prey were found at feeding depth on recent dives; in this case a bird such as the Shag, which can take several prey items on each dive (Wanless *et al* 1993a), might tend to dive for longer when prey are denser (or when they are less dense). Or the bird may be able to remember the depth at which prey are currently being found; for the Shag, because it feeds mainly on bottom-living species, that would amount to the same thing as remembering the depth of the water.

An animal which feeds regularly in the same sites may be able to predict prey density, water depth, or both, if it is able to recognize where it is. However, because both depth and prey vary quite rapidly in coastal waters, it would need quite precise location information, probably redetermining its position after each dive. This is not easily done in open water. When feeding close to land, the animal's best source of such information would be landmarks on shore. It is known that animals can use relatively long-range cues in order to navigate: for example, pigeons rely on landmarks for the last 50 km or so of homing (Matthews 1963), and, on a smaller scale, rats and squirrels use them to orient in mazes or to recover hidden food (eg. Biegler and Morris 1993; Macdonald, in press).

A second function of behaviour on the surface during feeding bouts could be social signalling. Unlike other members of its own genus such as the Spotted Shag of New Zealand, or other birds that dive for food around Lundy such as Razorbills or Guillemots, the Shag rarely dives in close proximity to others. It is unlikely, therefore, that it would have signals to indicate the presence of a good patch of prey. However, it might well be advantageous for birds to signal their intention to leave a feeding ground and fly away: birds might prefer to fly together for a number of reasons, including protection against predators, aerodynamic efficiency, or (particularly in the case of young birds flying with older ones) navigational guidance.

The present study aims to open the question of how Shags might be determining their position during a bout of dives, and what signals they might be giving. Our approach was to record all the behaviour that the birds showed on the surface during feeding bouts, paying particular attention to anything that might constitute inspection of landmarks, or that seemed to predict the end of a bout of dives.

METHOD

Study site

The study was carried out on Lundy. Observations were made during a one-week period during the spring of 1996. All observations were made at the Landing Bay, on the east side of the island. At the observation point, the coast ran approximately NNW to SSE; the sea to the north was relatively open, but to the south the coast curved round at a distance of approximately 0.5 km to enclose the Landing Bay. Observations were made at different times of day and states of tide, but we noted no major differences as a function of these variables, so they are not discussed further. Total observation time was approximately 35 hours, of which approximately 6 hours involved active data collection.

Procedure

Observations of Shags engaged in extended bouts of dives were made with the naked eye or with binoculars. The following four directional behaviours were recorded, as they occurred, into a hand-held dictaphone, for subsequent transcription and entry into a computer:

Face: The bird is on the surface, with its head pointing in the same direction as its body axis.

Look: The bird is on the surface, with its head turned at least 45° away from the direction of its body axis.

Dive: The bird dives into the water.

Surface: The bird emerges from the water after a Dive.

Takeoff: The bird flies away.

For each of these behaviours, the direction in which the bird's head was pointing was also recorded (for all behaviours except Look, this was also the direction of the body axis). The aim was to record it as one of the eight principal compass directions (North, North-East, East, etc). However, in some cases this involved a finer distinction than could in practice be made, and if in doubt the nearest of the four directions North, East, South and West were used. The North-South axis was taken, conventionally, as parallel to the coast-line; in practice this ran approximately NNW to SSE at the point of observation, and the plots of directions reported below are adjusted to take this into account.

In addition, the following non-directional behaviours were recorded in the same way: Head Shake, Head Lift, Head Drop, Tail Shake, Feather Shake, Feather Wash, Defecate, Wing Spread, Wing Flap, Preen with Bill, Dip Bill, Turn in a Circle, Land after Takeoff. These categories are self explanatory, but it should be noted that some of them (eg. Tail Shake, Wing Flap, Dip Bill) are carried out by Shags in a highly characteristic manner, and fulfil the definitions of a Fixed Action Pattern proposed by Lorenz (1932/1970).

Recording of a particular bird was terminated by Takeoff (without a subsequent Land), or by its mingling with other diving birds, or by its moving out of view. The cause of termination was recorded.

Note that we had no means of identifying individual birds, so that it is likely that some birds contributed more than one bout of dives.

RESULTS

A total of forty-five diving bouts were recorded, involving 355 dives. Twenty-three of the diving bouts were terminated by Takeoff (there were two additional Takeoffs after which the bird Landed again), eleven by the bird mingling with others, and eleven by

its moving out of view. Fig.1 shows the total frequencies of the other behaviours listed above.

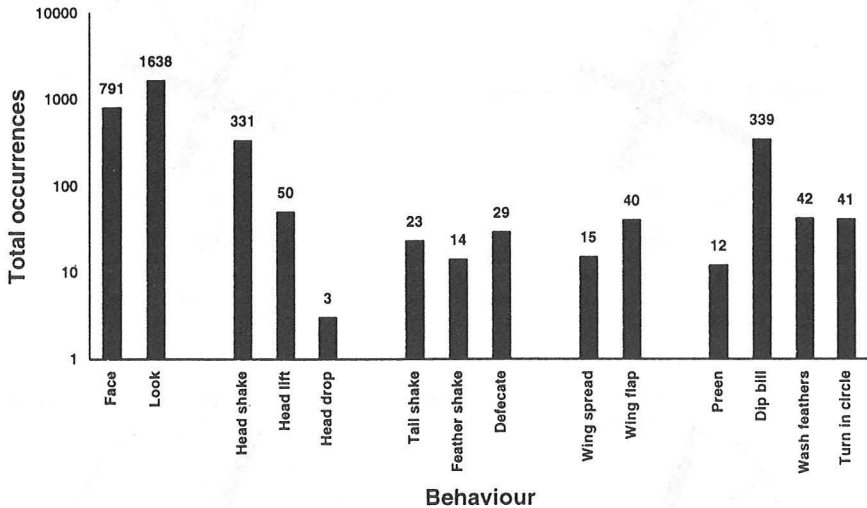


Figure 1: Total observed of each of the behaviours observed, other than Dive and Takeoff. Note the logarithmic scale on the vertical axis. Definitions of the behaviours are given in the text.

Analysis of directional behaviours

Fig.2 shows the distributions of the directions of the four directional behaviours, together with the direction of their mean vectors (calculated using the Oriana program: Kovach 1994) and the 99% confidence limits for their directions. Recall that in these plots the direction NNW to SSE is parallel to the coast, and that the four principal directions (North, East, South and West, actually NNW, ENE, SSE and WSW) were more likely to be used than the intermediate directions. The following features are immediately obvious.

1. For all four behaviours, North, East, South and West were recorded much more often than the intermediate directions. As explained in the Procedure section above, this was because these four principal directions were used in cases of uncertainty, so the predominance of the four principal directions should therefore be ignored. It can be seen that this predominance is greater for some behaviours (eg. Look, for which only the four principal directions were ever coded) than for others (eg. Dive), reflecting the fact the direction was easier to code for some behaviours than others.
2. The birds were more likely to Dive in Northerly than Southerly directions, and much less likely to Dive in Easterly (seaward) than Westerly (coastward) directions.
3. The birds were more likely to Face in Northerly or Westerly than Southerly or Easterly directions.
4. The birds were more likely to Look in Northerly or Easterly than Southerly or Westerly directions.
5. The birds usually made their Takeoff parallel to the coast (Northerly or Southerly), and virtually never towards the coast (Westerly).

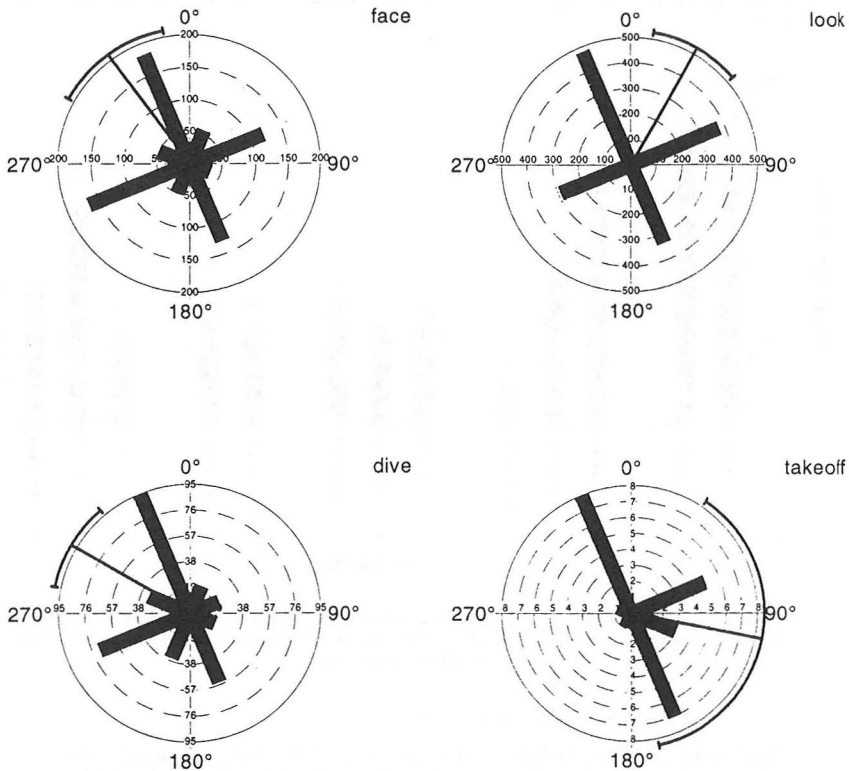


Figure 2: Circular histograms showing relative frequencies of directions of Face, Look, Dive and Takeoff. Narrower lines show the direction of the mean vector and its 95% confidence range. The coastline ran approximately NNW-SSE at the observation site.

6. The above four trends are statistically significant, in that the 99% confidence limits for the mean vectors lie within a single compass quadrant.

Analysis of non-directional behaviours

It was obvious to the observers that certain of the non-directional behaviours were particularly associated with the end of a diving bout. To quantify these trends, surface periods were divided into two categories: Surface-Dive intervals ($N=355$), and Surface-Takeoff intervals ($N=25$). Intervals terminated by a bird going out of view or mingling with other birds were discarded. Fig.3 shows the mean number of each of the non-directional behaviours occurring in each interval of these two types. It is clear that all of them are more likely to occur in intervals terminated by a take-off, and for several behaviours the difference is extreme, involving a factor between 10 and 100.

If all surface periods are regarded as independent observations, then the significance of the differences shown in Fig.3 can be assessed by a χ^2 test, comparing the proportions of Surface-Dive intervals and Surface-Takeoff intervals having at least one occurrence of each behaviour. On this basis, almost all the differences shown in Fig.3 are significant, with χ^2_1 values ranging from 10.17 to 239.03 for Wing Flap ($p < 0.01$ in

all cases); the only non-significant differences were those for Head Drop and Defecate. A more conservative statistical treatment would recognize that the observations within a single bout are not fully independent of each other, and that therefore we should compare mean behaviour rates from the two types of interval across bouts. This involves discarding data from all bouts where either no Takeoff was observed, or no complete Surface-Dive interval was observed, leaving only 19 of the forty-five bouts available for analysis. Inevitably this leads to a statistically less powerful test. However even on this basis the differences for Head Shake, Wing Flap and Wash Feathers were significant (two-tailed binomial tests, $p < 0.05$), and the trends for the remaining behaviours remained strong, falling short of significance only because of small sample size. It is clear that many of these non-directional behaviours could be used as highly valid signals that a Shag is about to finish a diving bout.

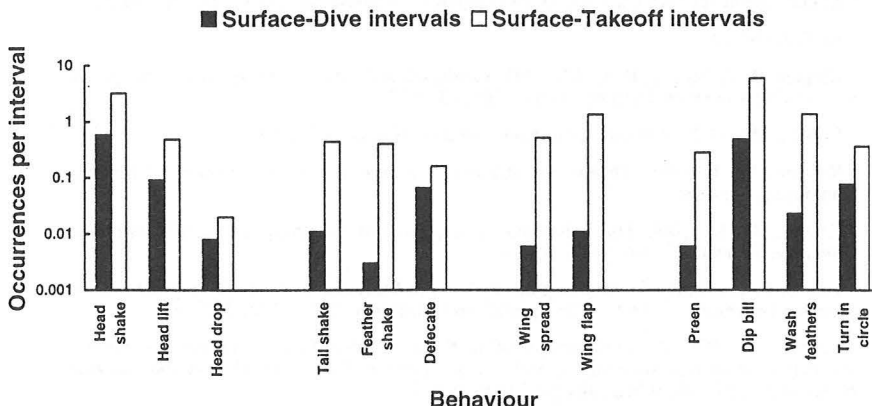


Figure 3: Rates of occurrence of non-directional behaviours in two types of surface intervals: Intervals between surfacing from a dive and diving again ("Surface-Dive", N=355), and intervals between surfacing from a dive and taking off without subsequently landing and continuing to dive ("Surface-Takeoff", N=25). Note the logarithmic scale on the vertical axis.

DISCUSSION

The Shags' surface behaviour during diving bouts showed clear directional selectivity. In part that affected the two behaviours that are an essential part of every diving bout, the dive itself (which was virtually never made outwards from the coast) and the takeoff at the end of the bout (which was usually parallel to the coast and virtually never towards it). The observed pattern of diving directions is what we would expect if the birds were referring to landmarks to maintain their position in the water. It could also be caused by adjustment to water currents (Lea *et al* 1996, mention that Pied Shags *P. varius* sometimes carried out extended diving bouts consistently facing into a strong estuarine current), though since observations were made in a range of tidal conditions, and dive direction did not seem to be correlated with the tides, this seems unlikely.

A preferred diving direction would necessarily impose a directionality on the birds' surface behaviour. The directions in which they tended to face were similar to those in which they dived, and may well have been determined by them. However, the directions in which the birds looked did not match the dive directions so closely: the birds frequently looked out to sea, though they neither faced nor dived in that direction. This pattern of results is what we would expect if the birds were looking around on

surfacing, and using the landmarks in view to re-orient themselves towards their preferred diving direction.

The directional behaviours, therefore, are consistent with the hypothesis that the birds use landmarks to remain on station during diving bouts, though alternative explanations are possible. The non-directional behaviours, on the other hand, are strongly concentrated in pre-takeoff periods, and clearly could be used as intention signals for flight. Analysis of social behaviour would be required to see whether other birds actually make use of the information these behaviours make available.

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