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OBSERVATIONS OF THE BOW-AND-MOAN DISPLAY PERFORMED BY THE KITTIWAKE GULL (*Rissa tridactyla*) ON LUNDY

By

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BACKGROUND

The first extensive account of the behaviour patterns and vocal repertoire of the Kittiwake gull (*Rissa tridactyla*) was published by Paludan (1955). He identified nine separate vocalisations and described the behaviours that accompanied them. However, these observations were made on a colony of ground-nesting Kittiwakes on Tyvholm, a somewhat unusual colony in that the majority of Kittiwake breeding colonies, including those on Lundy, nest on narrow cliff ledges.

Cullen (1957) conducted the earliest study of cliff-nesting Kittiwake colonies, observations being carried out on the Farne Islands from 1952-1956. She contrasted the Kittiwake with ground nesting relatives such as the Herring Gull (*Larus argentatus*) and the Lesser Black-backed Gull (*Larus fuscus*). Cullen showed how Kittiwakes differ from other gulls in two important ways: first, during the breeding season they nest on cliff ledges while outside it they are totally oceanic and stay out of sight of land; second, other sea birds may nest on ledges but these ledges are far wider than those used by the Kittiwake which are sometimes only four inches wide. Cullen (1957) argued that while many of the behaviour patterns and calls of the Kittiwake are homologous with the Lesser Black-backed Gull and the Herring Gull, the numerous constraints of occupying narrow cliff ledges and the consequent reduced risk of predation has led to specific adaptations in the biology and behaviour of the Kittiwake which are not found in other gulls. For example, a number of anti-predator behaviour patterns retained by ground nesting gulls, such as the Aggressive Upright Posture, are not observed in the Kittiwake. Indeed, it is not often that anti-predator reactions such as alarm calls are observed in Kittiwakes. In comparison with ground-nesting gulls, Kittiwakes allow intruders to come closer to the nest or nest-site before reacting and then often fly up without giving an alarm call at all. These observations are supported by Paludan (1955) who actually lifted a Kittiwake from its nest in the ground-nesting colony in Denmark. Thus the alarm call is heard much less often in a Kittiwake colony than in a colony of other ground-nesting Laridae.

Cullen (1957) further observed behavioural differences between the Kittiwake and other members of the gull family in and around their nest sites. The nest of the Kittiwake is shaped like a deep cup set on a mud foundation while the ground-nesting gulls nest is shallow and constructed of fibrous material and is altogether a looser structure. Ground nesting gulls remove egg shells from the nest and defaecate away from the nest, since to leave such clues around the nest could betray its location to predators. Obviously given the geographical location of the nest this is not such a problem to the cliff-nesting Kittiwake which leaves egg shells lying in the nest and defaecates over the rim of the nest, such that a white sheet of guano forms below each nest. Yet, despite such precipitous locations, Kittiwake colonies are still not predator free and as shown by Coulson (1968), greater breeding success is achieved by those nesting in the centre of colonies rather than at the edges, where the nests are more vulnerable to predators such as raptors, Ravens and Great Black-backed Gulls (*Larus fuscus*).

Tinbergen's classic paper, published in 1959, contains a review of research into gull behaviour and the description of a number of displays of the various gulls, specifically the Herring Gull group, the Hooded Gulls and the Kittiwake. Tinbergen points to the evolutionary origins, functions and causes of these displays and presents evidence to show that each of the displays has a separate signal function. Tinbergen further suggests that the most commonly observed single displays and display sequences are similar

throughout the gull family showing only small species-specific modifications, thus suggesting these behaviour patterns have a common evolutionary origin. While Tinbergen acknowledges that Cullen's study of the Kittiwake demonstrates how the behaviour and morphological peculiarities of this species have to do with its adaptation to breeding on sheer cliff faces, he limited his discussions to those behaviours that formed the basic core of all gull behaviours, thus concentrating on the similarities of the Laridae family rather than its differences.

Since Tinbergen's paper, very little research had been published on display behaviour of the Kittiwake until Daniels and Heath (1984), whose initial research was carried out on Lundy. They categorised the whole repertoire of Kittiwake displays and calls and attempted to explain the functional significance of each as well as its associated behaviour. The study covered a four year period 1979 - 1983 and was carried out in Puffin Gully. This is the site of the main Kittiwake colony on the island which at that time held over 400 nesting pairs.

Daniels and Heath argued that while the process of adaptation to cliff nesting led to the behavioural displays of the Kittiwake becoming less expansive and more inhibited, an expanded repertoire of vocal behaviour was evident which achieved similar signal function to that of expansive behavioural displays. Furthermore these researchers produced sound spectrographs of ten of the fourteen Kittiwake calls that have been identified; this provides an objective means of comparing and categorising calls.

The purpose of the present study is to clarify the function of the Bow-and-Moan display of the Kittiwake. The earlier findings from research concerning this display are somewhat ambiguous and occasionally contradictory (eg. Daniels and Heath 1984; Danchin 1991).

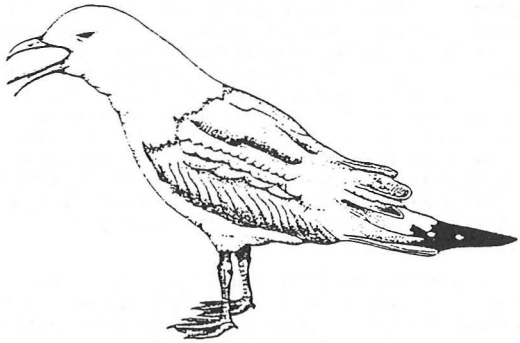

Fig.1 Line drawing of the Bow-and-Moan Display of the Kittiwake Gull

The Bow-and Moan posture is a somewhat intimidating posture. the neck is extended, curved and laterally flattened, The eyes are narrowed and slitted while the bill is open and the tongue lowered; slow, rhythmic bowing movements are made. A very soft cooing sound is uttered throughout the downward and upward components of the display with the Kittiwake sometimes reorientating its entire body to face in a different direction between bows (after Daniels and Heath 1984).

The earliest documentation of the Kittiwake's Bow-and-Moan behaviour was by Paludan (1955) who called it the "Cooing Posture" because of the similarity of the sound with that of a pigeon. In view of the small number of observations of this behaviour pattern it proved difficult to determine the underlying releasing cause(s). However Paludan suggested that the posture was connected with the maintenance of territorial rights and is one of threat and intimidation. Paludan further observed that

birds who were trespassing some distance from an occupied nest-site could prolong the time to inevitable attack by the incumbent bird(s) if the Cooing Posture and associated vocal behaviour were emitted. Following the trespasser's departure the nest owners would then adopt the same posture and show similar vocal behaviour. Tinbergen (1959) also makes reference to the Kittiwake's Bow-and-Moan posture noting its similarity to the Mew Call posture adopted by the Lesser Black-backed Gull but with a bending-down element added. He suggests that this posture and call is uttered in various situations including hostile situations, during pair formation and during the incubation and care of the chicks.

Daniels and Heath (1984) are in accord with Paludan (1955) when stating that the Bow-and-Moan display is usually performed in hostile situations and is clearly used in the maintenance of territorial rights. It is most commonly used by nest owners to threaten or deter potential intruders, with such intruders, on occasion, also adopting the display. The display was often followed by attack if an intruder failed to heed the warning. However, Daniels and Heath suggest that the Bow-and-Moan repertoire is not confined to the nest site, having observed its occurrence when Kittiwakes were competing for the use of a rock on which to rest and preen and also amongst birds foraging for nest material. They further state that this display is contagious and spreads from one bird to all the birds in the vicinity. These authors also state that both male and female Kittiwake's will emit the Bow-and-Moan posture but never simultaneously. A further study by Daniels, Heath and Rawson (1984) contained specific observations of the vocal behaviour emitted by the Kittiwake immediately preceding a bird's departure from the nest and partner. The findings from this study show that Bow-and-Moan display preceding nest-departure was not observed at all during the incubation stage (ie. when eggs are present in the nest), however it was observed to occur infrequently during the pre-incubation stage and at slightly higher frequencies during the post incubation stage when the squabs or chicks are in evidence. During the early chick-rearing period the display is given briefly by the departing parent before leaving the nest. As Daniels and Heath state, this is somewhat paradoxical in that nest relief is not a hostile situation.

More recent work by Danchin (1987) emphasises the importance of establishing the social status of the birds in order to be able to understand their behavioural patterns. In this study post-landing behaviours were divided into two categories: those used mainly by Owners; and those by Non-Owners. If a bird had built a nest on the site it was allocated the status of Owner, otherwise it was considered to be a Non-Owner. According to Danchin, the Bow-and-Moan occurred as a post-landing behaviour mainly in Non-Owners, a very low frequency being observed in Owners. This contradicts the observations made by Daniels and Heath who state that it is most often shown by nest owners. Danchin goes on to describe how, during initial landings at a potential nesting site, the Kittiwake is usually silent and adopts post-landing displays which are similar to those of the alert and preparing-for-flight sequences. However following return to the same nest-site the Kittiwake displays the Bow-and-Moan more frequently upon landing. This appears to contradict Danchin's previous claim that the Bow-and-Moan is a Non-Owners behaviour, since frequent return to the same nest-site appears to infer ownership.

The main conclusions that can be drawn from Danchin's (1987) study are that Bow-and-Moan occurs in two main circumstances: the first being a dispute between two individuals unable to reach each other; and the second being before flight away from the nest-site, for example during nest-site relief. These observations are in accord with the observations made by Daniels and Heath who suggest that it is most commonly used when an intruder lands close to the nest but out of range of the Owners beak. More recently Danchin (1991) claims that when the Bow-and-Moan is performed during nest relief it is performed by the male. He claims that when the Bow-and-Moan was shown as a display prior to leaving the nest-site it was due to males in aggressive situations involving a third bird participating in the nest-site relief from a proximate site. In this 1991 study, Danchin was concerned with the social significance of six of the Kittiwake's displays including the Bow-and-Moan. Contained within this study are further elaborations of the contexts in which the Bow-and-Moan display was observed. For example, when a landing bird shows Non-Owner behaviour, neighbouring birds were observed to display Bow-and-Moan behaviour as were birds landing on sites that were

not their own. It was further observed to occur prior to departure and preceding flights leading to aggression towards a neighbour. To further complicate the interpretation of the Bow-and-Moan display in the Kittiwake, Daniels, Heath and Stevenage (1994) have recently observed the Bow-and-Moan display occurring spontaneously on the sea north of Lundy prior to the occupation of the breeding sites.

Research suggests that there are several contexts in which the Bow-and-Moan display has been observed to occur. Despite the ambiguities and contradictions contained within the research, the Bow-and-Moan display would appear to predominantly function as a Resource Holding display. The present study aimed to clarify the situations in which the Bow-and-Moan display occurs and thus to establish the motivational basis and the function of the display. Furthermore the research programme sought to clarify the Owner/Non-Owner ambiguities contained in previous research and thereby resolve the paradox of why an ostensibly Resource Holding Potential display is performed during non-hostile situations, specifically nest-relief and departure.

METHOD

The colony studied was at Puffin Gully where the largest breeding colony on Lundy is situated; there were approximately 30-40 breeding pairs early in April 1994, prior to the total colonisation of the breeding site when approximately 200 pairs occupy the ledges.

Observation commenced when the Kittiwakes returned from rafting, generally at midday. Observations were made from a vantage point on one side of the breeding gully at a distance of approximately 7-8 m, so binoculars were not needed. Prior to data collection, and to enhance inter-experimenter reliability, the experimenters observed and agreed upon exactly what constituted the Bow-and-Moan display. Furthermore the experimenters agreed to designate as nest sites those areas of the cliff face marked by prominent white flags of guano. Kittiwakes repeatedly landing on such sites were classified as Owners; those landing on unmarked sites were classified as Non-Owners.

Two different methods of data collection were selected. First, focal-bird-sampling, as described by Altman (1974). This involved selecting a Kittiwake for a half hour observation period. Data collection entailed recording every behaviour that the Kittiwake emitted during this period. It was expected that such a method would provide a sequential account of the context in which the Bow-and-Moan occurs. The second method involved scanning the colony and selecting for observation any Kittiwake who was seen to be performing the Bow-and-Moan display. A stopwatch was used to ensure that the duration of each display was recorded, and that data were collected with regard to the behaviour immediately following the Bow-and-Moan display as well as the context of the behaviour, which included threat, nest-site arrival/departure, and location within the colony.

It is known from Coulson's work (1968) that the centre of a Kittiwake colony suffers a lower risk of predation and is therefore more successful for breeding; competition for sites, therefore, is fierce. Given that most previous research suggests that the Bow-and-Moan display is a Resource Holding Potential display, it was hypothesised that a higher frequency of Bow-and-Moan would be observed in the much sought after centre of the breeding colony. An initial perusal of the data suggested that there appeared to be a difference in the frequency of the Bow-and-Moan display at the centre of the colony relative to that at the edge. To investigate this further, a method discribed by Altman (1974) as 'one-zero sampling' was used to collect binary data from the centre and the edge of the colony. Twenty nest sites were selected from the centre and edge of the colony and these were observed for five minute periods, at ten minute intervals, for a period of one hour. Each occurrence of the Bow-and-Moan display observed was scored as one and no other data was recorded from that nest site during that five minute period. To all other nest sites where there was no occurrence of the Bow-and-Moan a zero was allocated. These frequency counts were analysed using the Mann-Whitney U statistic.

RESULTS

To determine the context, either situational or behavioural, that most frequently

preceded the Bow-and-Moan display, the focal bird data were initially analysed using the Fisher Exact statistic (Table 1). Prior to this analysis the observed behaviours were coded. The result of this analysis was highly significant ($p<.0001$), showing that the Bow-and-Moan at this stage of the breeding season is significantly more likely to occur following return to the nest than following any other behaviour.

Table 1: Fisher Exact analysis of the behaviour preceding the Bow-and-Moan display.

	Any other time	Before Bow-and-Moan	Total
Any other behaviour	55	2	57
Return to nest-site	9	9	18
Total	64	11	75

A further analysis of the focal bird data was undertaken to discover whether the Bow-and-Moan display regularly preceded any other behavioural sequence (Table 2). Again the Fisher Exact statistic was used to analyse the data and the result of this analysis was highly significant ($p< .01$). This shows that Downward Choking is significantly more likely to follow the Bow-and-Moan display than is any other behavioural display.

Table 2: Fisher Exact analysis of instances of behaviour superseding the Bow-and-Moan display.

	Any other time	After Bow-and-Moan	Total
Any other behaviour	56	11	67
Downward Choking	8	9	17
Total	64	20	84

To investigate whether any of the behavioural variables observed significantly predicted the duration of the Bow-and-Moan display, data were analysed using Best Regression. Prior to the regression analysis an Analysis of Variance was conducted to ensure that bird number was not a significant predictor of display length, since this would invalidate the regression analyses. No relationship was found and a Best Regression procedure was used to find the regression model that best fitted the data. However the model was a poor fit and no significant predictors of the length of the display were isolated.

A further binomial test was applied to all of the focal data regarding occurrences of the Bow-and-Moan display prior to nest-site departure to determine whether these were threatening situations or not. There were fifteen occurrences of nest departure which were preceded by the Bow-and-Moan display, of which fourteen were preceded by a threatening situation. The result of the binomial test was highly significant ($p<.001$). Therefore, when the Bow-and-Moan display precedes nest departure, the situation is almost invariably threatening (eg. when a resident is being threatened by a neighbour).

A Mann Whitney U test was applied to 'centre' versus 'edge' frequency data and there was shown to be a highly significant difference ($W=254.5$, $P<0.0001$), such that the Bow-and-Moan display occurs with most frequency in the centre of the colony. No significant difference was found in the frequency of occurrence of the Bow-and-Moan display between Owners and Non-Owners.

DISCUSSION

Following perusal of the earlier research of the Bow-and-Moan display of the Kittiwake, it became apparent that this research contained certain contradictions with regard to whether the display was predominantly an Owner or Non-Owner behaviour. This study found no significant difference in the frequency of occurrence of Bow-and-Moan display between Owners and Non-Owners; thus nest-site ownership was not found to be a significant predictor of this display. It was however found that the position of nest sites within the colony was a significant predictor of the frequency of the Bow-and-Moan display with there being a significantly higher frequency of this display in the centre areas of the colony as opposed to the edges. This finding is in accord with the Bow-and-Moan being a Resource Holding Potential display since, as was initially observed by Coulson (1968), the centre of a Kittiwake colony is more successful for breeding and hence is more highly sought after.

Daniels and Heath (1984) were the first to make the observation that the Bow-and-Moan display sometimes preceded nest-site relief. Such an observation is paradoxical because nest-site relief/departure would not appear to be a hostile situation, whereas most evidence suggests that the Bow-and-Moan is a hostile display. This research has confirmed that the Bow-and-Moan precedes nest-site departure and further analysis of the data collected has shown that it was predominantly emitted in threatening situations such as confrontation with a neighbour or Non-Owner. These results go some way towards eliminating the apparent paradoxical findings of previous research while lending more support to the Bow-and-Moan functioning primarily as a Resource Holding Potential display. Nevertheless these results appear to raise a further paradox in that it would appear unusual to leave a nest, and possibly partner, unprotected in what is obviously a threatening situation. This may support Zahavi's (1987) theory of signal selection, from which it can be argued that departing the nest in a threatening situation may function as an honest signal of Resource Holding Potential, successfully advertising the Owners ability and intention to return. It would be interesting to investigate this further.

Two further significant findings from this research suggest that the Bow-and-Moan display, at this time of the breeding season, occurs with most frequency as a landing behaviour and is predominantly followed by Downward Choking. Downward Choking is an aggressive signal and given that it frequently supersedes the Bow-and-Moan display, adds further credence to the Bow-and-Moan functioning primarily as a Resource Holding Potential. It was noted by the researchers that when Non-Owners performed the Bow-and-Moan display it was rarely followed by Downward Choking. Unfortunately there were insufficient data points for this to be analysed statistically. Furthermore while analysis of the data on the duration of the display gave no significant results it was noted that the duration of the display appeared to be considerably longer in Non-Owners than Owners, though this could not be demonstrated statistically, again due to a lack of data points. Therefore, these two areas require more research particularly with respect to the duration of the Bow-and-Moan display of Non-Owner Kittiwakes.

An unusual observation was made during the course of this research concerning a Kittiwake apparently going through the motions of the Bow-and-Moan display but with no moan being emitted. Given the rarity of such an observation it was decided by the researchers to consult a more experienced observer who confirmed the observation. Furthermore, a pair of Kittiwakes were seen to perform the Bow-and-Moan towards each other before commencing the greeting ceremony, so contradicting Danchin's (1987) statement that the Bow-and-Moan is only performed by a male Kittiwake. However, to support this claim, further observations are required to facilitate gender identification in such a situation.

The results described here are both interesting and useful in that they dovetail neatly with previous studies giving clarification of the contradictions and paradoxes that have evolved. Despite the growing data base and the advances in understanding that have been made of Kittiwake behaviour during the last few years, many questions remain unanswered. Given the colonies of Kittiwake on Lundy, this is considered a suitable place at which to address these questions.

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