

FREQUENCY AND FUNCTION OF THE HEAD-TOSSING DISPLAY IN THE KITTIWAKE (*Rissa tridactyla*)

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ABSTRACT

Over a period of ten years, an investigation comprising four studies was made of the Head-Tossing display of the Kittiwake gull (*Rissa tridactyla*). The first study sought to establish (a) the frequency of occurrence of Head-Tossing in relation to Courtship-Feeding and Copulation; and (b) the comparability of the two main breeding sites investigated, in three displays, at particular times of the breeding season. Three further studies drawing data from both sites showed that the Head-Tossing display emitted by a single partner elicited five discrete responses in the receiving partner in addition to those of Courtship-Feeding and Copulation. All the displays were noted and described as Outcomes and two of these responses, Head-Shaking and Low-Intensity or Aggressive Choking, appeared to have an inhibitory effect on further interaction. A third study sought to elucidate whether, during a mutual display of Head-Tossing in both partners, (a) body orientation and/or (b) the duration of the mutual display affected the Outcome. Orientation of the displaying pair had no effect on the Outcome, but it was shown that the Outcome was related to the duration of the display, in that the shorter the display (<41 seconds) the more likely Courtship-Feeding or Copulation would occur as opposed to other outcomes. The final study investigated the effect of the gender of the initiating bird on the Outcome and revealed that male initiated Head-Tossing was likely to lead to Courtship-Feeding, whereas female initiated Head-Tossing predominantly led to Copulation.

INTRODUCTION

Head-Tossing is one of the main courtship displays in the Kittiwake gull. The display was first reported and described by Paludan (1955) in a ground nesting colony of Kittiwakes. Paludan named the display Head-Bobbing and whilst observing that the display preceded Courtship-Feeding and Copulation, reported that, "it has not been possible to perceive any sound during the performance of the ceremony" (*ibid*,5). Tinbergen (1959), drawing together observations made on different species of Laridae, re-christened the display naming it Head-Tossing, pointing out that a soft sound accompanies the head movement. The first complete description of Head-Tossing was made by Daniels (1983), Daniels and Heath (1984) and referred to briefly by Danchin (1988). In short, the display begins when one or other bird in a pair adopts a hunched posture (see fig. 1) and throws its head upwards with an even regularity of 1-2 movements per second, interspersing this rhythmicity with a gentle jabbing or probing around the base of the partner's bill. A high-pitched (4KHz) sound is emitted throughout the display which may be represented as tseep-tseep-tseep; Danchin refers to, "...the Peeping Call which usually accompanies Head-Tossing" (1988,444). Tinbergen (1959) has suggested that the display originated in the food-begging movements of Kittiwake squabs. Certainly, the posture and the accompanying vocalisation emitted by adult birds resembles the posture and vocalisation made by Kittiwake squabs when soliciting food from a parent. It is obviously a display which communicates physiological/motivational state and possibly serves to bring partners into hormonal synchrony whilst also indirectly serving as a communicative signal within the colony, to bring all members of the colony into synchronous breeding activity.

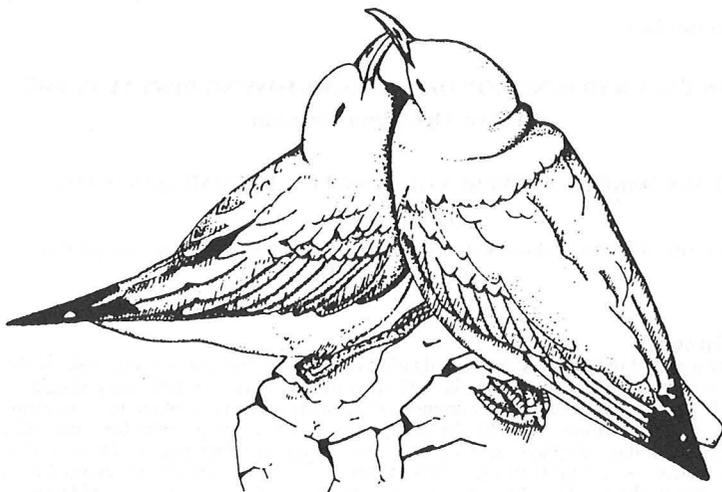


Fig. 1: The Head-Tossing display in the Kittiwake (*Rissa tridactyla*)

Mutual Head-Tossing in partners precedes both Copulation and Courtship Feeding, but Head-Tossing by a single partner may elicit responses other than Head-Tossing. The display has never been observed in solitary Kittiwakes when alone on the nest-site, but has been observed in isolated birds on the sea, where Kittiwake flocks form rafts prior to occupying the breeding-cliffs (Daniels, Heath and Stevenage, in press).

Copulation in the cliff-nesting Kittiwake has been described by Cullen (1957), the female squatting to accommodate the male rather than standing as occurs in other Larids and in the ground-nesting Kittiwake.

Courtship-Feeding in cliff-nesting Kittiwakes involves one partner regurgitating food from the crop and allowing the other partner to carefully take the food directly from its mouth, rather than regurgitating on to the ground as in the case of the Herring Gull (*Larus argentatus*).

Four questions intrigued us and therefore shaped the investigation:

1. Is there any pattern or structure to the appearance of the Head-Tossing display throughout the breeding season?
2. What is the Outcome, following Head-Tossing in a single partner, as opposed to mutual Head-Tossing in both partners?
3. Is there a causative relationship between the mutual display made by both partners and Courtship-Feeding and Copulation?
4. If such a relationship exists, what determines the Outcome of either Courtship-Feeding or Copulation?

STUDY AREAS AND METHODS

An opportunity arose during 1981 to study Head-Tossing behaviour in the cliff-nesting Kittiwake throughout the entire breeding season, when these mainly oceanic birds occupy breeding-cliffs from April through to mid-August. Further studies of the display followed over a period of ten years up to 1991, in an attempt to uncover the nature and function of the Head-Tossing display.

Two study sites were used over a period of ten years from 1981-1991. The first and largest was Lundy where around the north and north-west coasts of the island, Kittiwakes are located at Puffin Gully (approximately 220 breeding pairs), Long Roost (fifty breeding pairs), Kittiwake Gully (twenty breeding pairs), St. John's Stone (twenty breeding pairs) and Jenny's Cove (twenty breeding pairs). There are other small colonies around the island, but these are not as accessible for observation.

The second site used was at Hope's Nose, South Devon, where during the 1980's there have been approximately 200 breeding pairs. Since 1989 this colony has declined markedly in numbers to only twenty breeding pairs in 1992.

Study I The frequency of Head-Tossing, Courtship-Feeding and Copulation throughout the breeding season.

LUNDY - 1981

Observations were made from April to mid-August. They began at 0700 hrs and continued throughout the day until 1700 hrs. Each week sampling was done on at least three days and at most five days depending on weather conditions. Twenty nest-sites were selected and observed for a period of 5min during which incidences of Head-Tossing, Courtship-Feeding and Copulation were recorded. The sampling method used was that of binary sampling (Altmann 1974), namely whether or not the particular display occurred in the 5min period. Following a 15min interval, a further, different, twenty nest-sites were selected and similarly sampled for all three displays. In this way, the frequency of occurrence of all three displays were recorded for each of 71 days throughout the breeding season April to mid-August, a total of 106 days although the incidence of all three displays was negligible from mid-July. No nest-site was sampled on more than one occasion throughout all the studies.

HOPE'S NOSE - 1985

Similar observations were made at this site in South Devon. However, because of the data acquired during 1981, the sampling here did not begin until the start of the second week of April and continued only until the third week of May. Data were similarly collected on three or four days per week making a total of 21 days from a possible 54 days.

Study II Behaviour elicited by Head-Tossing in one partner only

LUNDY AND HOPE'S NOSE - 1989

During the second and third weeks of April and the first and second weeks of May, one of a pair of Kittiwakes displaying Head-Tossing behaviour was located within the colony, using Focal-Animal Sampling (Altmann 1974). This bird was denoted Bird A (the signaller). The sequence of behaviour which followed was then recorded - ie. Bird B's (the receiver's) response, then Bird A's subsequent response to Bird B. Finally, the Outcome was recorded which was the behaviour eventually exhibited by both birds, (ie. Courtship-Feeding, Copulation or other behaviours). If after 3min there was no Outcome the observation was discontinued. All samples were independent in that no nest-site was sampled on more than one occasion.

Study III What determines the Outcome when both partners display Head-Tossing?

LUNDY AND HOPE'S NOSE - 1990

In this study, an attempt was made to discover what factors determine the Outcome, following mutual Head-Tossing in both partners. Given that during Courtship-Feeding and Copulation, different postures are adopted by partners in relation to each other it was thought that the posture adopted by the partners during mutual Head-Tossing possibly affected the Outcome. Partners, within limits, either commenced mutual Head-Tossing with their bodies in parallel or facing each other, so the orientation of the birds at the start of the mutual display was noted. The duration of the mutual Head-Tossing was also recorded from initiation of the display to the commencement of the Outcome. If there was no Outcome after 3min of mutual Head-Tossing, the observation was terminated. Data was collected during the second and third weeks of April and the first and second weeks of May.

Study IV The effect of the gender of the bird initiating Head-Tossing

LUNDY - 1991

Data were collected using Focal-Animal Sampling during the appropriate weeks of April and May. The gender of Bird A, the bird initiating the Head-Tossing interaction, was recorded in relation to the Outcome.

Very few of the birds in this colony were ringed, so identification of gender was facilitated by spraying a weak solution of a red, water soluble food colouring over the parts of the colony being observed. The gender of focal birds was then determined by watching until the next copulation. In this way the gender of 55 birds was determined.

RESULTS

Study I

LUNDY - 1981

Head-Tossing, Courtship-Feeding and Copulation follow a similar pattern throughout the season with activity in all three displays reaching peaks during the second and third weeks of April and the first and second weeks of May (fig 2a). The correlation coefficients using the raw data for Head-Tossing with Courtship-Feeding and Head-Tossing with Copulation are 0.77 and 0.58 respectively ($P < 0.001$ for both), confirming the close association between these displays noted but not quantified by previous workers (eg. Paludan 1955, Tinbergen 1959).

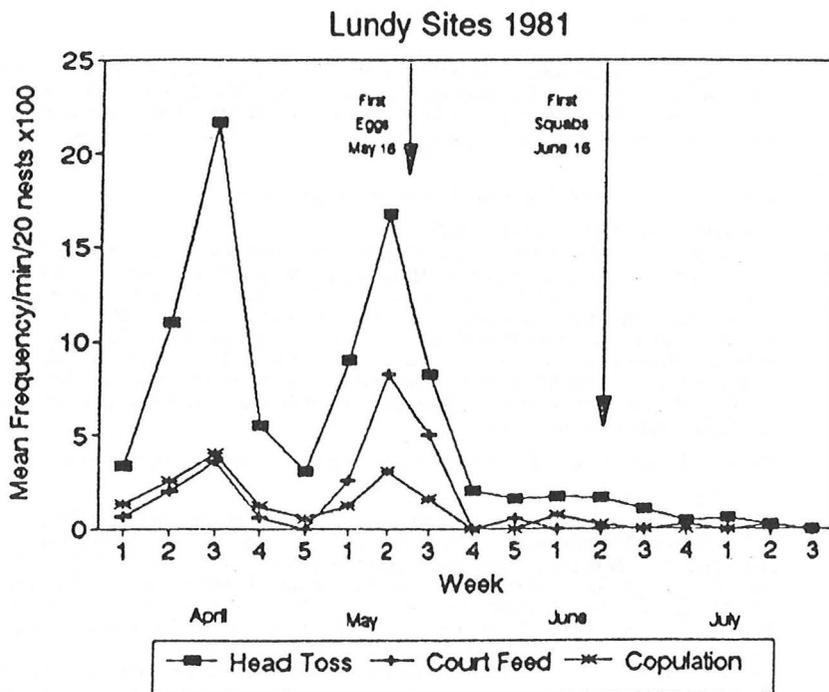


Fig. 2a

Fig. 2b

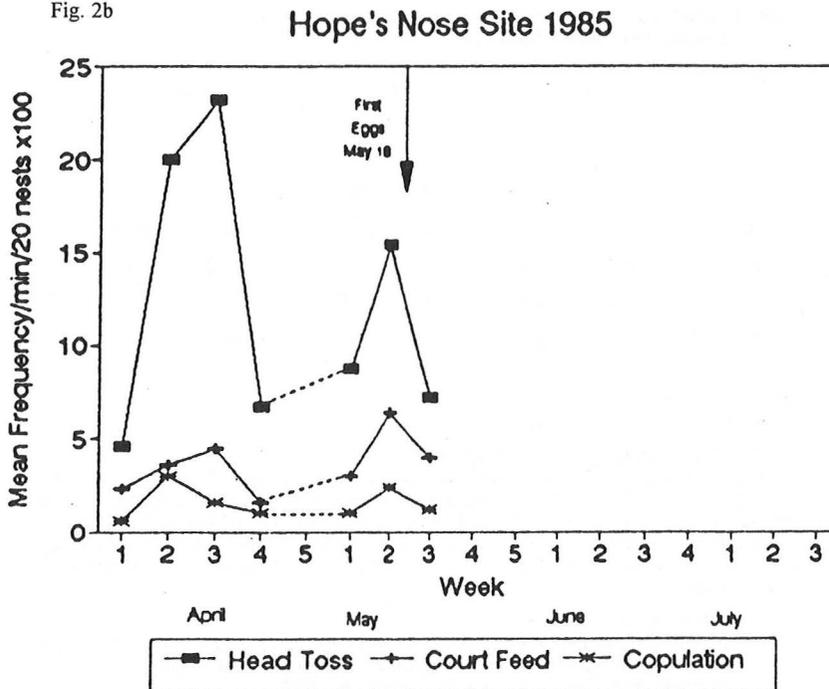


Fig. 2: Showing the distribution of all three displays over the entire occupation of the breeding cliffs for Lundy (2a) and over April and May for the Hope's Nose (2b). Each 'Week' is the mean of 4 or 5 days data except week 5 in April which was not sampled at Hope's Nose and consists of only two days data at Lundy.

HOPE'S NOSE - 1985

Since all three displays reach their greatest level of occurrence during the second and third weeks of April, and the first and second weeks of May on Lundy, sampling at Hope's Nose was confined to these particular weeks. No data were collected during the fifth week of April, hence the dotted line connecting the fourth week of April with the first week of May in fig. 2b. All other points represent means per 3 or 4 days per week. The data showing the frequency of Head-Tossing, Courtship-Feeding and Copulation are also given in fig. 2b and confirms the earlier finding that all three displays are frequently in evidence at these times of the breeding season. The correlation coefficients using the raw data for Head-Tossing with Courtship-Feeding and Head-Tossing with Copulation are 0.73 and 0.5 $P < 0.001$ respectively.

Given these data all subsequent observations of the three displays were confined to the middle two weeks in April and the first two weeks of May. A series of t-tests (see table 1) carried out on the raw data collected at Lundy and Hope's Nose revealed no significant differences in the frequency of occurrence of Head-Tossing, Courtship-Feeding and Copulation. The two sites are therefore considered to be comparable.

**Table 1 Significance of the difference between means
Lundy (1) v Hope's Nose (2).**

	HT		CF		Cop	
	1	2	1	2	1	2
N	24	24	24	24	24	24
Mean	10.77	12.27	3.22	3.63	2.1	1.54
SD	6.42	7.26	2.69	1.57	1.09	0.86
t	1.19	1.07	1.32	0.93	1.41	0.9
P	ns	ns	ns	ns	ns	ns

Study II

LUNDY AND HOPE'S NOSE - 1989

Despite revealing a significant association between Head-Tossing, Courtship-Feeding and Copulation, Study I provided no evidence regarding causality. Casual observation had indicated that Head-Tossing emitted by one of the partners did not necessarily lead to mutual Head-Tossing or to either Courtship-Feeding or Copulation. At least five displays other than the two latter, had been noted in response to Head-Tossing:

1. **Facing Away**
In this display the receiver (Bird B) turns the head away from the signaller (Bird A) and buries the bill beneath the carpal joint. This display is discussed at length by Cullen (1957) and by Tinbergen (1959).
2. **The Pre-Departure Display**
In the Upright posture, Bird B in this instance utters a call which often heralds departure from the nest-site/nest. This display has been studied and reported in detail by Daniels *et al* (1984) and discussed by Danchin (1991).
3. **Head Shaking**
This display has recently been described by Danchin (1991) as consisting of "vigorous head shakes in an horizontal plane". The accompanying vocalisation is a "jik-jik-jik" sound which Danchin (1991) labels the K-call and Paludan (1955) as "Coughing". Daniels and Heath (1984) report that the display intersperses with Head-Tossing in one or both partners before or after copulation and in the male sometimes during copulation.
4. **Low Intensity Choking**
Not to be confused with the more rhythmic advertising display of the male Kittiwake, known as Downward Choking, this display intersperses with bouts of aggressive behaviour and can be exhibited by both male and female Kittiwakes. The display has been described in detail elsewhere, eg. Daniels *et al* (1984) and Danchin (1991), although the latter author prefers the term "Trembling Choking" (*ibid*,73).
5. **The Greeting Ceremony**
Described most vividly first by Paludan (1955) and later by Heath *et al* (1982), this graceful ceremony is performed by partners on the nest-site upon reunion or sometimes apparently spontaneously. Throughout the display each bird utters the Long-Call whilst bowing to the partner and often linking necks. The display ends with Upward Choking (Tinbergen 1959).

Of a total of 231 independent observations made (table 2), Head-Tossing is the response to Head-Tossing on 46% of the occasions, whilst Head-Tossing combined with Head-Shaking was the response on 22% of the occasions (table 2). Low-Intensity-Choking occurred in 18% of the occasions.

Table 2 Responses made by Bird B when Bird A initiates Head-Tossing.

	N	%
Head-Tossing	104	46
Head-Tossing and Head-Shaking	51	22
Low-Intensity-Choking	42	18
Head-Shaking	18	8
Facing-Away and Pre-departure Display	16	7

Table 3 Subsequent behaviour of Bird A to Bird B's response to Head-Tossing

Bird B's Behaviour	Bird A's subsequent behaviour				
	HT	HT + HS	LIC	GC	NR
HT	76	14	8	14	0
HT + HS	17	6	11	10	0
LIC	3	2	0	31	0
HS	10	5	3	0	0
NR	10	2	11	0	0

Key: HT = Head-Tossing; HS = Head-Shaking; LIC = Low Intensity Choking; GC = Greeting Ceremony; NR = No Response (N=231). Excluding the NR category $X^2_{12} = 132.513$, $P < 0.001$

Whereas a Head-Tossing response by Bird B facilitates further Head-Tossing in Bird A, Low-Intensity-Choking and Head-Shaking both appear to inhibit further Head-Tossing by Bird A (table 3). Even when Head-Shaking intersperses with Head-Tossing, the likelihood of Head-Tossing continuing in Bird A is diminished.

Mutual Head-Tossing can proceed to Courtship-Feeding or to Copulation or to Low-Intensity-Choking (table 4). Further, although Courtship-Feeding occurs as an Outcome more often than either Copulation or Low-Intensity-Choking, the latter occurs as an Outcome more often than Copulation (see Discussion).

Table 4 Eventual Outcome of Mutual Head-Tossing

Outcome	N	%
Courtship-Feeding	59	36
Copulation	38	23
Low-Intensity-Choking	47	29
Other Outcomes	18	11
Facing-Away		
Greeting Ceremony		
Predeparture Display		

NB Of the 162 independent observations, both Low Intensity Choking and Courtship Feeding occur more frequently than copulation.

Study III

LUNDY AND HOPE'S NOSE - 1990

Neither orientation of the partners' bodies at the commencement of mutual Head-Tossing, nor the length of time of the mutual display, had any effect on Outcome (table 5). What can be said is that at this time of the season, the longer the mutual display continues, the more likely it is that Facing Away, the Predeparture Display or the Greeting Ceremony will be the Outcome and the less likely it will be for either Courtship-Feeding or for Copulation to occur. In other words, as can be seen in Table 5, if either of the latter are to be the Outcome, then the mutual display has to be of less than 41 seconds duration.

Table 5 Orientation at commencement of Mutual Head-Tossing and Mean Duration of the display

	In parallel			CF	Facing Cop	Other Outcomes
	CF	Cop	Other Outcomes			
N	16	19	4	22	19	2
Mean Duration in s	36.2	39.3	165	35.2	41	153

Key: CF = Courtship Feeding; Cop = Copulation; Other Outcomes comprises Facing Away, the Predeparture Display, the Greeting Ceremony and Low Intensity Choking.

Study IV

LUNDY - 1991

The gender of the bird initiating the display is the main factor which determines the Outcome (table 6). Male initiation is more likely to result in Courtship-Feeding whereas female initiation predominantly leads to Copulation.

Table 6 Outcome in relation to gender of the initiator of Mutual Head-Tossing

Gender	N	CF	Cop	N.R.
Male	28	22	3	3
Female	27	4	20	3

Key: CF = Courtship Feeding; Cop = Copulation; NR = No Response.

DISCUSSION

In order to determine the function of the Head-Tossing display in the Kittiwake, a large number of independent observations needed to be made. Of the two breeding sites studied, neither alone provided sufficient pairs of birds to accommodate such an investigation. Therefore, the first study sought to establish comparability between the two sites. The results indicated that the sites were indeed similar in terms of the behaviours exhibited at particular times of the breeding season and in terms of the frequency of occurrence of the various behavioural displays being investigated (see fig.2). This finding established, it was then possible to derive the necessary independent data from both sites, over the necessarily protracted period of the investigation. Although the data collected in the first study revealed that Head-Tossing is closely related in time to both Courtship-Feeding and to Copulation, it was not possible to argue from the data or postulate any causative links between the displays. As a result, the second study sought to uncover the total range of possible responses to Head-Tossing displayed by one partner in the presence of the other. Of the six different responses observed to occur in the receiving partner, Head-Tossing was the most likely response. Furthermore, Head-Tossing as a response facilitated further Head-Tossing, whereas Low-Intensity-Choking (or Trembling Choking, after Danchin 1991) and Head-Shaking appear to inhibit further displays of Head-Tossing.

When both partners exhibit mutual Head-Tossing, the Outcome was either Courtship-Feeding, or Copulation, or Low-Intensity-Choking. If the latter was the Outcome then no further Head-Tossing occurred. This is an intriguing finding, since Zahavi (1982) has cogently argued that all such displays are analogues of internal motivational states. Thus, it is possible although such signals are prone to corruption (Dawkins and Guilford 1991), that Low-Intensity-Choking communicates a state of motivation that is either asynchronous to, or in some way is incompatible with, those motivational states communicated through the behaviour of Head-Tossing Courtship-Feeding and/or Copulation. Further, from the data (table 4) it is evident that Low-Intensity-Choking occurs, as a response to Head-Tossing, more often than Copulation. Thus, Low-Intensity-Choking as a display, may well be an important controlling factor in determining the Outcome as it is in sanctioning departure from the nest (Daniels *et al* 1984).

Whether Courtship-Feeding or Copulation followed mutual Head-Tossing was investigated throughout Study III. Here it was shown that whilst orientation of the partners bodies at the initiation of mutual Head-Tossing was not *per se* important in determining Outcome, the duration of the display was very important. Mutual Head-Tossing of less than 41 seconds resulted in either Courtship-Feeding or Copulation, with no significant difference detectable in duration between either, as an Outcome. If, however such a mutual display continued for more than 41 seconds, then the interactive behaviour became less orientated towards procreation and more directed towards either, (a) a reaffirmation of the pair-bond, when the Greeting Ceremony was performed, or (b) possible disinterest, evidenced by Facing-Away or by the Pre-Departure Display.

How revealing, yet how simple the results of Study IV were and, why didn't we start here? Of course, as was expected, the gender of Bird A in initiating the interaction of Head-Tossing was an important factor in determining the Outcome. Male initiation

generates Courtship-Feeding whilst female initiation is more likely to lead to Copulation (table 6). If one accepts these data, then it is clear that it is the female who dictates whether or not Copulation will take place by communicating through the Head-Tossing display. Furthermore, reference to figs 2a and 2b reveals that the increase in frequency of the display within the two colonies possibly serves the function of bringing the entire colony into synchronous breeding behaviour.

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