Rep. Lundy Field Soc. 43

EVIDENCE FOR PAIR-BOND FORMATION IN KITTIWAKES (Rissa tridactyla) PRIOR TO OCCUPATION OF THE BREEDING SITES ON LUNDY

By

Dr. D. DANIELS

Department of Psychology, Washington Singer Laboratories, University of Exeter, Devon EX4 4QG

INTRODUCTION

Previous studies of the Kittiwake colonies around Lundy (e.g. Daniels 1983; Heath *et al* 1982; Daniels and Heath 1984; Daniels *et al* 1984) have concentrated entirely on the behaviour of these enigmatic birds on the breeding sites at Puffin Gully, Kittiwake Gully, Long Roost, St. John's Stone and Jenny's Cove. Of British gulls (Laridae) the Kittiwake *(Rissa tridactyla)* is the most oceanic, coming to places like Lundy only to breed between April to August. Whilst on land the Kittiwake nests colonially on north facing, sheer cliffs, making nests on extremely narrow ledges. Since observations have focussed on Kittiwake behaviour on land, it has been widely assumed (e.g. Cullen 1957; Chardine 1983; Coulson and Thomas 1983) that the cliff face or breeding site is the only place where pair-interactions occur. Furthermore, Coulson and Thomas (1983) argue that Kittiwakes, once bonded, remain loyal breeding partners for as long as 17 years. It is further assumed that the pair split up during the winter and only re-form the pair-bond upon returning to the breeding site. Older Kittiwakes are said to return first, followed by younger birds and finally by the first-time breeders. However, the observations reported below suggest that these assumptions are not strictly true. Certainly for the Lundy breeding sites, since Kittiwakes are present off-shore around Lundy, *in flocks* at least one month prior to occupation of the breeding sites around the island. Moreover behavioural interactions within these off-shore flocks include many of the aggressive and courtship displays described previously (Daniels and Heath 1984; Daniels *et al* 1984; Danchin 1987) for birds on land.

Whilst some studies have mentioned the presence of Kittiwake flocks off-shore at the start of the breeding season (e.g. Maunder and Threlfall 1975), this surprisingly, is the first systematic study reporting behavioural interactions within the flocks whilst the birds are still off-shore.

METHOD

The main colony for breeding on Lundy is located at the North End within the confines of Puffin Gully, where, in 1990 there were approximately 220 breeding pairs. The flocks were observed through March of that year when there was no evidence of occupation within the gully, (i.e. there was no guano or nest material present on the cliff faces). However, the gully was fully occupied by the end of the first week of April and on all subsequent dates after that time.

During March, the distance of the flocks off-shore varied from 150-800m, and these were always formed, initially, directly in front of the entrance to the gully. Although tide and wind inevitably moved the flock away from this position, e.g. to the area of sea, north of the North Light, the flock would fly up and reform in the original position, in front of the gully.

From a vantage point above Puffin Gully, observations were made using 10 x 50 binoculars and a 16 x 32 telescope. The former allowed the number of birds within the flock to be counted, whilst the latter facilitated observation of individual birds within the flock. The number of birds within the flock were counted at 15 minute intervals between 10.00 and 17.00 hours each day and these data are given in fig. 1. The behaviour observed in individual birds are given in Tables 1 and 2. The method employed to record

these data was that of Focussed Sampling (Altman 1974) which involved locating a bird which was emitting the familiar Long Call (here called the Aquatic Long Call) of the Kittiwake and, observing the subsequent behavioural interactions between birds on the sea.

As can be seen from Table 1, the most frequent response to Aquatic Long Calling was another Aquatic Long Call. So bird A would emit the Aquatic Long Call, birds B, C, D, etc. would respond with similar calls. More often than not, it can be seen from Table 1 that only one bird would respond and enter the Greeting Ceremony in which birds bow to each other and cross necks whilst continuing to emit the Long Call (Daniels and Heath 1984). Then, again using Focussed Sampling, observations were made of the interactive behaviours which followed this particular interaction. Proceeding in this way, it was possible to determine the various types of behaviours which followed Aquatic Long Calling, organise the data successively by weeks to examine trends and changes and then determine the frequency with which specific behaviours occurred, following the Greeting Ceremony exhibited on the sea.

RESULTS

The data on the size of the flock throughout the day and over the period of the study are given in fig. 1. It is evident from fig. 1, that not only does the size of the flock increase throughout the month, but it also increases from week to week indicating the gradual arrival of more and more birds. Flock density was variable, but birds were spaced at typical distances from each other of 2-3 Kittiwake lengths.

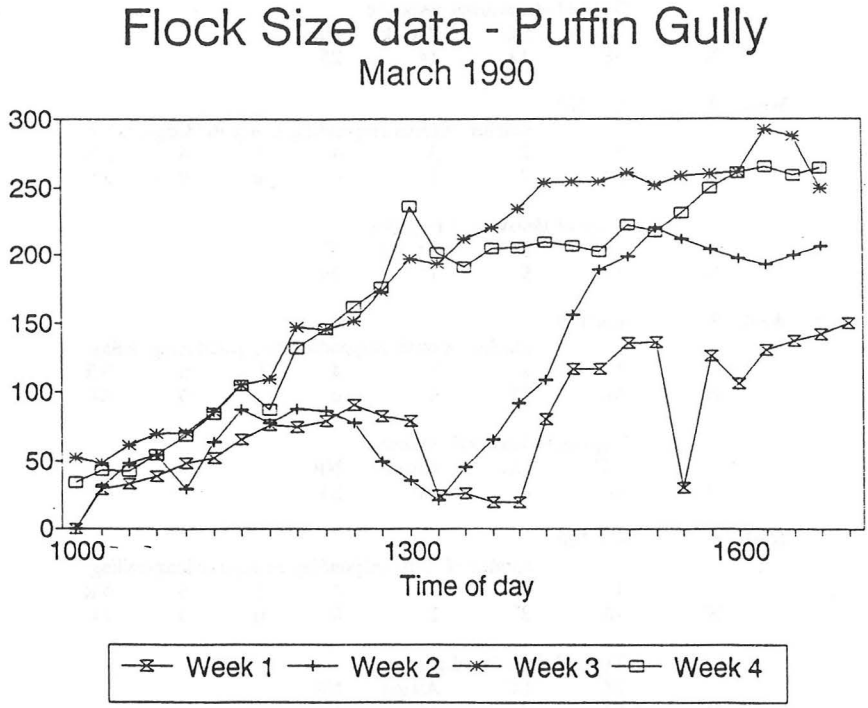

Figure 1: Showing the increase in the size of the flock throughout the day and over the period of study.

a. INTERACTIONS WITHIN THE FLOCK

Most behavioural interactions on the sea were initiated by the Aquatic Long Call, although both the Bow-and-Moan and Downward Choking displays (see Daniels and Heath 1984, for a full description of these displays) were observed to occur spontaneously in individual birds. However, it was the former (i.e. the Aquatic Long Call) which captured interest and it and subsequent interactions were quantified.

The Aquatic Long Call differs in a number of ways from the terrestial Long Call emitted at the breeding site (i.e. on the cliff face). In the latter case it is predominantly uttered upon the return of one of the pair when it forms the basis of the very graceful Greeting Ceremony. On the sea however it was notable that Kittiwakes never emit the call upon landing on the sea and make no immediate attempt to interact with neighbours on the water. The call at sea is spontaneous and emitted whilst the bird is paddling vigorously and turning its body in different directions, as if to broadcast the sound. The number of birds responding to this display is given in Table 1.

TABLE 1

Puffin Gully Sites

Week 1		n = 100						
		number of birds responding to aquatic long-calling						
		1	2	3	4	5	6	NR
	N	57	9	5	1	3	0	25
		Type of Behavioural response						
		GC	LC	Attack	NR			
	N	48	13	14	25			
Week 2		n = 100						
		number of birds responding to aquatic long-calling						
		1	2	3	4	5	6	NR
	N	63	7	1	0	0	0	29
		Type of Behavioural response						
		GC	LC	Attack	NR			
	N	51	9	11	29			
Week 3		n = 100						
		number of birds responding to aquatic long-calling						
		1	2	3	4	5	6	NR
	N	61	11	4	0	0	0	24
		Type of Behavioural response						
		GC	LC	Attack	NR			
	N	54	8	14	24			
Week 4		n = 100						
		number of birds responding to aquatic long-calling						
		1	2	3	4	5	6	NR
	N	76	8	2	0	0	0	14
		Type of Behavioural response						
		GC	LC	Attack	NR			
	N	63	7	16	14			

GC = Greeting Ceremony, LC = Long-Call, NR = No Response

As can be seen from Table 1, 100 observations were recorded for each week of March making a total of 400 observations. Table 1 further shows that Aquatic Long Calling largely led to Aquatic Greeting Ceremonies and the incidence of such interactions increased as March progressed. The calling birds moved towards each other arriving, either face to face or in parallel then commencing the mutual rhythmic movements of head and neck characteristic of the ceremony, whilst continuing to emit the call. As in the terrestial Greeting Ceremony, the interaction terminates with Upward Choking though this is less pronounced and less vigorous in the aquatic version.

The main courtship display of the Kittiwake is the Head Tossing Display (Daniels and Heath 1984; Danchin 1987) in which one bird will adopt a hunched posture and throw its head upwards with an even regularity (1-2 per sec) interspersing this rhythmicity with gentle jabs or probes around the base of the partners bill. Throughout the display a high-pitched tseep-tseep-tseep sound is emitted reminiscent of the sound made by Kittiwake squabs when soliciting food from the parent. The display during April leads to either Courtship Feeding, when food is taken from the partners crop, or to Copulation. Occasionally Courtship Feeding did occur ont he water during March,, but Copulation was never observed. However, Aquatic Head Tossing, when it occurred, commenced immediately after the Greeting Ceremony ended and continued for up to two minutes.

TABLE 2

Puffin Gully Site: Types of behaviour which follow the aquatic Greeting Ceremony

	N	Head Tossing	Bill Dipping	Pre-Departure Call	No Further Behaviour
Week 1	48	14 (29.16%)	21 (43.75%)	2 (4.16%)	11 (3.91%)
Week 2	51	19 (37.25%)	20 (39.21%)	3 (5.88%)	9 (17.64%)
Week 3	54	17 (31.48%)	21 (38.88%)	5 (9.25%)	11 (20.37%)
Week 4	63	24 (38.09%)	22 (34.92%)	5 (7.93%)	12 (19.04%)

$x^2 = 34.514$; df = 9' $p<0.001$

Table 2 shows the frequency with which three explicit behaviours followed the Aquatic Greeting Ceremony. These three were Head Tossing, Bill Dipping and the Pre-Departure Call. The Pre-Departure Call has been described in detail by Daniels *et al* (1984) and will therefore not be discussed here. Bill-Dipping is a display hitherto unreported in the literature. It sometimes follows the Aquatic Greeting Ceremony in pairs when both birds dip their bills very rapidly into the sea followed by a shake of the head. This could be an aquatic version of Low Intensity Choking (Daniels and Heath 1984). Occasionally, a slower, more rhythmic Bill-Dipping occurred and preceeded the Aquatic Long Call. Bill-Dipping is an intriguing display; it is known that ritualized preening and bathing form the basis of many courtship displays in other birds e.g. the Anatidae. Since this study was completed, further observations have been made of this unique display and will form the basis of a future report.

A Chi-squared analysis was carried out on the data presented in Table 2 and revealed that these values could not have been due to chance. In other words there is a distinct pattern to the behaviour observed, and these were displays not made randomly.

DISCUSSION

It is clear from the data presented above that courtship behaviour in the Kittiwake is not confined to the breeding sites. The main courtship displays of this gull, the Greeting

Ceremony and Head Tossing have both been observed to occur within flocks on the sea and in the vicinity of the breeding site. These observations bring into question the supposition that Kittiwakes perform all their pair-bonding behaviour within the confines of the breeding site.

It is also clear from these data that occupation of the breeding site in these conditions is severally different from that described by Coulson and Thomas (1983). In the colony studied and described by these latter workers, the Kittiwakes build nests on the window ledges of warehouses situated on the north bank of the River Tyne some miles from the sea. There, it is said, the Kittiwakes arrive at the breeding site in small groups over the period December to April (Coulson and Thomas 1985).

Kittiwakes live for up to 22 years and tend to retain the same mate over a period of up to seventeen years (Coulson 1972). However, some birds do indeed change mate, either through death of a partner, or by "divorce". Asynchronous return to the colony between pairs is considered to be the mechanism for a change of mate (Coulson and Thomas 1983). Furthermore, these workers also note that "divorce" is more common among mates that fail to breed. Such failure perhaps stems from the same incompatibility that results in partners' asynchronous return to the breeding site.

At both breeding sites studied here, most if not all members of the colony were present 14-16 days prior to the occupation of the breeding sites. Furthermore, the move to the cliffs was completely synchronised, and all breeding sites were occupied fully by the end of the first week in April. Therefore, the mate-choice mechanism proposed by Coulson and Thomas (1983) cannot be applied in this situation.

Cullen (1957) in her classic study of Kittiwakes postulated that Kittiwakes, unlike ground-nesting gull species, do not go to neutral ground or to pairing territories prior to the breeding season. Rather, males were said to go directly to the nesting ledges and there advertise for females whilst repelling males using the Downward Choking display. The immediate occupation of a site by male occupation, was attributed to (a) the Kittiwakes "fear of land" and (b) the severe competition for nesting-sites. However, the present study has revealed that Kittiwakes do not return to the breeding site directly, but remain offshore, in flocks, for at least one month, prior to the synchronised occupation of the cliffs. Although individual male Kittiwakes could have moved to the ledges at any time during that month, none did. Thus, occupation of the breeding site was clearly a "colonial" decision, possibly linked to hormonal synchrony resulting from mutliple behavioural interactions.

It is likely that the offshore Kittiwake flock is equivalent to the pre-breeding gathering of ground-nesting Larids on neutral ground, and for example the Lapwing (Vanellus vanellus). Furthermore it is possible that Kittiwake partners remain in contact outside the breeding season, as in some passerine species (Witkin and Ficken, 1979) which would obviate any protracted pair-bond formation each and every year. However, the establishment of hormonal synchrony could be achieved through similar courtship displays and interactions with neighbours.

Since pair interactions occur away from the breeding site, recognition of partners is a necessary precondition. Individual recognition is most obviously achieved through vocal recognition (Wooller 1978; Falls 1982). However, exactly how Kittiwakes discriminate between kin and partner is not known and will form the basis of further research.

ACKNOWLEDGEMENTS

The author would like to thank the many students who helped in collecting the data reported and discussed in this paper. Most noteable of these has been Sarah (Beanie) Hodgeson and Suzanne Davis. Bill-Dipping was first observed in the Kittiwake by Jason Heath in 1981 who spent, at that time, long hours observing and categorising Kittiwake behaviour - but for great reward.

Thanks too are gratefully offered to Mrs Rachel Kirby, Experimental Officer at the Department of Psychology at Exeter, for her thoroughness in data-handling and for her expertise in the use of Quatropro. Such expertise led to Figure 1 and from a mass of

bird spattered, rain-smudged digital data. She is a gem of enormous worth.

Finally, one must say that were it not for the University of Exeter who fund this research, it would not continue.

REFERENCES

Altman, J. 1974. Observational study of behaviour - sampling methods. *Behaviour* 49, 227-267.

Chardine, J.W. 1983. Aspects of the behaviour of Kittiwake pairs during the pre-egg stage. PhD thesis, University of Durham.

Coulson, J.C. 1972. The significance of the pair-bond in the Kittiwake. *Proceedings XV International Ornithological Congress* 424-433.

Coulson, J.C. and Thomas, C.S. 1983. Mate choice in the Kittiwake gull. In Bateson, P. (ed.) *Mate Choice* 361-376. Cambridge University Press.

Coulson, J.C. and Thomas, C.S. 1985. Changes in the biology of the Kittiwake Rissa tridactyla: a 31-year study of a breeding colony. *Journal of Animal Ecology* 54, 9-26.

Cullen, E. 1957. Adaptation in the Kittiwake to cliff-nesting. *Ibis* 99, 275-302.

Daniels, D. 1983. Vocal Behaviour in the Kittiwake Gull (Rissa tridactyla). *Annual Report of the Lundy Field Society* 34, 13-15.

Daniels, D and Heath, J. 1984. The calls and displays of the Kittiwake (Rissa tridactyla). *Devon Birds* 37, 4-13.

Daniels, D., Heath, J. and Rawson, W. 1984. A declaration of intent in the Kittiwake gull (Rissa tridactyla). *Animal Behaviour* 32, 1151-1156.

Danchin, E. 1987. The behaviour associated with the occupation of breeding site in the Kittiwake gull (Rissa tridactyla). *Animal Behaviour* 35, 81-93.

Falls, J.B. 1982. Individual recognition by sound in birds. In Kroodsma, D.A., Miller, C.H. and Quellet, H. (eds.) *Acoustic Communication in Birds* 2, 237-277.

Heath, J., Slater, A.M., Daniels, D. and Merrifield, S. 1982. Duration of vocal behaviour during the greeting ceremony of the Kittiwake. *Behaviour Analysis Letters* 2, 221-225.

Lorenz, K. 1951-53. Comparative studies on the behaviour of the Anatidae. *Avic. Mag.* 57, 58.

Maunder, J.E. and Threlfall, W. 1972. The breeding biology of the black-legged Kittiwake in Newfoundland. *Acta. Zoological Cracov.* 16, 581-668.

Witkins, S.R. and Ficken, M.A. 1979. Chickadee alarm calls: Does mate investment pay dividends? *Animal Behaviour* 27(4) 1275-1276..