Average clutch size for a Kittiwake *Rissa tridactyla* colony on Lundy

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Introduction

Kittiwake populations on Lundy have been in decline for many years. Davis & Jones (2007) give population data from 1939 to 2004. In 1939 there were 3,000 occupied nests. The next year for which there was a complete survey was 1950, when there were 1,387 occupied nests. Between 1950 and 1973 there were a further 11 complete surveys and the numbers peaked at 2,026 and dropped to 718, with some fluctuations. Since 1981 (with 933 occupied nests) there has been a steady decline (eight complete surveys), to a population of 148 occupied nests in 2004. The Seabird Register for 2008 and 2013 adds to this story, giving figures of 151 and 127 occupied nests (see Price, Slader & Booker, 2013; Figure 1).

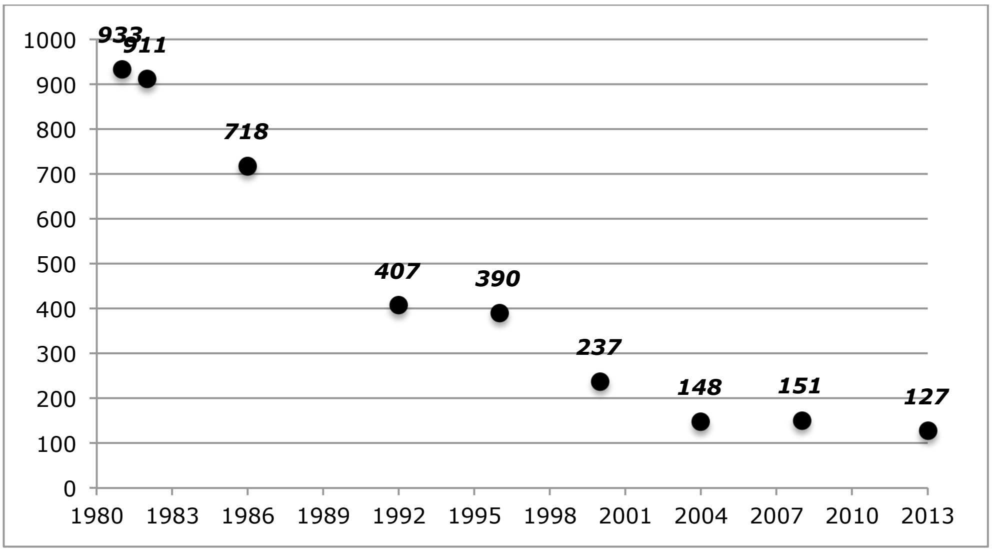

Figure 1: The declining trend in Kittiwake numbers on Lundy over nine surveys from 1981 to 2013; adapted from Price, Slader and Booker, 2013.

Since 2004 the most active area for Kittiwake nesting has been between the Pyramid north to St James' Stone on the Atlantic west coast of the island. This report presents data for a colony in that region collected during June 2015.

Methods

Between 1 and 4 June 2015, initial observations were made from a safe vantage point above the scramble-restricted areas south of the Kittiwake colony at Aztec Zawn. On 5 June, the colony was mapped from the same position. The map was hand drawn in two separate sections, and nests and potential nest sites (perches) numbered. The map relied upon a few distinctive geological features and the clustering patterns of the sites. This minimalist approach reduces confusion when the colony is viewed from different angles. The map was found to agree with a 2013 image used by the island warden and her team, and subsequently new photographs were taken to confirm the accuracy of the map. The nest numbering system is my own.

Each day, from 6 June until 12 June 2015, an initial census sweep was made to assess the status of the colony. Standard RSPB codes were used (Table 1) to ascertain the number of incubating adults and nest contents.

Table 1: RSPB bird monitoring codes for a Kittiwake survey (adapted from Gilbert, Gibbons & Evans, 2011, *Bird Monitoring Methods*)

Code	Description
I	Apparently incubating adult
c/n	Clutch of n eggs
c/0	Empty, well built nest with adult in attendance
c/x	Well built nest with adult standing, contents unknown

Once the census was completed, more detailed clutch data was collected using opportunity sampling. This involved visually scanning the colony for movement of adults at the nest and then using binoculars, a telescope or a 500mm lens attached to a digital SLR in order to yield an egg count for each nest. For example, an adult standing up from an apparently incubating position or an adult being replaced at the nest by a partner could provide sight of nest contents. To this end I used cues such as adults calling from the nest to predict the arrival of a second adult, and constantly scanned the colony looking for movement. As I gathered data the number of nests scanned would decrease.

This survey work was mostly conducted in the middle of the day (see Table 2). Opportunity sampling only was conducted on 5 June 2015, once the map had been produced.

Table 2: The time each RSPB census was begun at Aztec Zawn throughout one week in June 2015, and the time at which opportunity sampling for nest contents was stopped on the same days. Opportunity sampling commenced immediately after the census was complete. Initial weather conditions during the sample have also been informally noted. Weather conditions were consistent each day.

Date	Start time of census	Stopping time of opportunity sampling	Weather
5 June	Not available	Not available	Not available
6 June	10:00	13:50	Strong westerly, broken cloud, bright, cool
7 June	13:10	15:50	Light westerly, bright, warm, calm sea
8 June	12:10	Not available	Not available
9 June	09:30	12:35	Still, clear, bright, mild
10 June	11:30	12:35	Light breeze, clear, warm, sea calm
11 June	12:08	15:55	Light breeze, overcast, mild, sea calm
12 June	11:37	13:28	Gentle breeze, mild, moderate cloud cover, bright

Results

The census and clutch data will be described, followed by a calculation of average clutch size per nest across the colony, based on this data. All data were analysed using IBM SPSS version 21 on an iMac (OS 10.10.3).

Census data

A total of 71 sites were recorded during the overall survey. Some of these sites changed from nests to perches, and from perches to nests during this period, and some were abandoned and then re-adopted. Table 3 takes account of this with the introduction of the 0 and Perch categories. This is in part due to continuing nest-building activity. From 5–8 June there were 65 recorded sites; from 9–10 June there were 68, and for the remaining days there were 71. Recorded sites include nests and perches.

Inevitably, some data are missing due to difficulties of observation but also because some sites were only discovered during the survey and the map had to be amended. Statistical analyses (available upon request) showed that missing data were evenly spread across 0,1 and 2 egg categories, such that these observed clutch sizes were equally likely to have missing data.

Table 3a: The frequency of census categories across the seven days of census taking. Note that some categories have been added to those listed in Table 2. Perch indicates sites that had previously been noted as a nest on the map (constructed on 5 June 2015) but were now seemingly being used only as perches. 0 indicates complete absence of adults and eggs. Also note that on 11 June one nest site (nest 48) hatched one chick. This chick had been recorded as an egg (c/1) on both 11 and 12 June: since no other chicks hatched during this survey, the addition of a new category was thought unnecessary.

Date	Perch	0	I	c/0	c/1	c/2	c/x	Missing
6 June	3	-	55	6	-	-	-	7
7 June	3	-	54	7	-	-	1	6
8 June	3	3	49	10	-	-	-	6
9 June	5	5	48	5	2	2	1	3
10 June	6	5	44	9	3	-	1	3
11 June	5	6	52	4	2	-	1	1
12 June	4	2	44	11	4	1	3	2

Table 3b: The percentage of census categories across the seven days of census taking. This percentage is calculated from the number of observations made, therefore excluding missing data. All other amendments from Table 3a apply.

Date	Perch	0	I	c/0	c/1	c/2	c/x
6 June	4.7	-	85.9	9.4	-	-	-
7 June	4.6	-	83.1	10.8	-	-	1.5
8 June	4.6	4.6	75.4	15.4	-	-	-
9 June	7.4	7.4	70.6	7.4	2.9	2.9	1.5
10 June	8.8	7.4	64.7	13.2	4.4	-	1.5
11 June	7.1	8.6	74.3	5.7	2.8	-	1.4
12 June	5.8	2.9	63.8	15.9	5.8	1.4	4.3

Estimating average clutch size

Two methods were used to estimate the average clutch size per nest for the colony: the best day (method 1) and the last count (method 2). These methods help to understand how successful the colony is in a given year.

Method 1: 11 June saw the least missing data, with almost two thirds of 71 sites being successfully surveyed. On that day, 41.3% of the observed sample had zero eggs, 26.1% had one, 28.3% had two and 4.3% had three eggs. 74.3% of the observed sample were apparently incubating during the census sweep, and contributed to the majority of the egg count.

Table 4 displays the relationship between the initial census allocation on 11 June and the egg count. Forty-two eggs were recorded on that day across 27 sites, and 19 empty sites; a sample of 46 sites from a possible 71.

Table 4: Data from 11 June showing the number of each category of eggs (zero, one, two, three) within each of the census categories they were assigned to. Looking at the Zero egg count one can see that 6 zero egg allocations were associated with an entirely empty site classification in the opening census sweep; 8 were associated with an apparently incubating adult; 4 with an empty well built nest, with an adult in attendance; and, 1 with a well built nest with adult standing and contents unknown. Note that the one chick has been recorded as [One/c/1], as discussed.

	Census category				
	0	I	c/0	c/1	c/x
Egg count					

Zero	6	8	4	0	1
One	0	10	0	2	0
Two	0	13	0	0	0
Three	0	2	0	0	0

Method 2: A final egg count variable was produced by taking the last available egg count for each nest. So, if the last count for a particular site was on 12 June that would be recorded. But if there were missing data for 12 June I would go back in time to the next day that did have data and record that. By this method there were 56 eggs across thirty-seven sites in the colony (17 one egg, 19 two egg and 1 three egg sites); 23 empty sites, all associated with adults; and, 11 sites with missing data. Three of the missing data sites were perches and the remaining eight had apparently incubating adults on them at some point.

Calculations: Using these two methods we can estimate the clutch size per nest, c_n, by dividing the number of eggs observed, e_o, by the total number of sites observed, s_o, (i.e. excluding those with missing data), such that:

$$c_n = e_o / s_o \qquad (1)$$

This yields the following estimates:

Method 1: 42/46 = 0.913 eggs per nest
Method 2: 56/60 = 0.933 eggs per nest

Assuming a total colony size, N, of 71 active sites (where all perches are turned to nests), and no further predation or egg loss, we can estimate a total colony egg count, E, of between 64.82 and 66.24 eggs using equation 2:

$$E = c_n \times N \qquad (2)$$

Using both methods we can see that between 41% and 38% of the sites counted were empty. It is not clear whether these were all failed nests, but some were definitely predated during the sampling period (see below). This data can be used to estimate the total number of active sites. 41% of 71 possible sites leaves 29.33 possible empty sites, and therefore 41.67 active sites. Using equation 2 to calculate E this gives a value of 38.04 eggs for the entire colony, a value close to that of e_o in method 1. Using the 38% estimate yields a prediction of 41.07 eggs, again close to the value of e_o in method 1. Nonetheless, neither value is close to the e_o of 56 using method 2.

These calculations make it clear that a number of sites contain more than one egg, and make it likely that in some instances not all eggs in a nest will have been visible. Given this I would favour using the upper estimate of method 2, and I would treat this as slightly conservative. Nonetheless, I doubt the colony is at replacement productivity even if all eggs are converted to chicks.

Finally, I attempted to estimate the amount of laying that occurred during the study period. According to Coulson (2011) the gap between laying eggs is usually up to two days, with a maximum of three days. To this end I looked through the data to determine whether or not egg numbers had increased over a one, two or three day interval and noted 13 potential laying events, 29 definite no laying (so, final clutch size) and 20 instances where there was insufficient data to make a decision. This last category would mean future laying was still possible. There were nine cases of missing data, meaning the total sample was 62 sites.

Field notes

Predation: The only predation witnessed was a number of raids by a single Great Black-backed Gull *Larus marinus*. I cannot be certain that it was the same gull on each occasion, for no rings were present, but the regularity of the arrival of a single bird around mid-morning and mid-afternoon each day suggests that it was the same. Predation by this species accounted for the loss of three eggs in peripheral nest sites, and a number of attempts in similar sites were observed. These sites were easier for such a large bird to access as they bordered less steep terrain, so that the gull could walk very close to the nest and then clumsily hop down and use its wings to maintain position just long enough to grab eggs before falling into flight. The adults whose nests were predated put up little resistance, and probably due to their peripheral position no general colonial alarm was raised. Nests that had been predated were still observed and it was noted on each occasion that within 24 hours adults were seen to court and copulate at the nest site.

Disputes: Neighbour disputes between Kittiwakes are common. A notable dispute involved the displacement of an incubating adult (nest 62) by another pair of Kittiwakes. One of the incoming pair then took over the nest and continued incubating two eggs until the original adult returned and removed that adult, and its partner perching to the side. It was possible to determine this as the original adult continuously circled the nest once displaced and the whole interaction took place within the field of vision provided by my binoculars.

One nest was abandoned and its eggs were taken during that period. Later the site was reoccupied. Another nest was briefly abandoned when the wings and sternum of a predated adult Kittiwake fell onto it, covering the eggs. The next day, two adults arrived, failed to remove the remains, and copulated on top of them. The following day the remains were gone, the original eggs appeared to remain, and the adults began placing some new nest material over those eggs.

Neighbour analysis

Having seen that peripheral nests were predated, I calculated the number of neighbours each site had. A neighbour was defined as a site within pecking distance of the focal site. This was gauged through direct observation of interaction and of the colony together with the map and photographic images. Nests immediately adjacent to one another met this criterion. Those that did not were isolated nests (such as nest 62) and nests that were above or below another at such a distance that any interaction would mean moving partially from the nest and stretching to reach. This definition will in no way capture the entirety of interactions or benefits of colonial living but it was chosen as a measure due to the lack of group defence noted during predations (see above). In other words, denser nesting might lead to greater group defence.

Coulson (2011) has developed a centre and edge classification for colony structure for similar analyses. The birds that arrive at the colony first at the beginning of the season form the centre and the edge are then the second wave of arrivals that nest around this core. As this was not observed for this study I have developed this neighbour method as an alternative.

Sites in the colony proved to have zero, one, two and three neighbours by this analysis and I was able to group final egg counts, as calculated in method 2 above, under these categories. Sites with missing data for final egg counts were excluded, giving a total of 60 sites. Figure 2 displays the raw data. A chi-square analysis revealed no significant differences in final egg count across neighbour categories (available upon request). This means that final clutch size, as calculated for this study period, is evenly distributed across the colony and is not a function of the number of neighbours within pecking distance. However, it does not mean that the causes of egg loss are evenly distributed across the colony. Coulson (2011) notes that eggs are sometimes lost during neighbour disputes, for example.

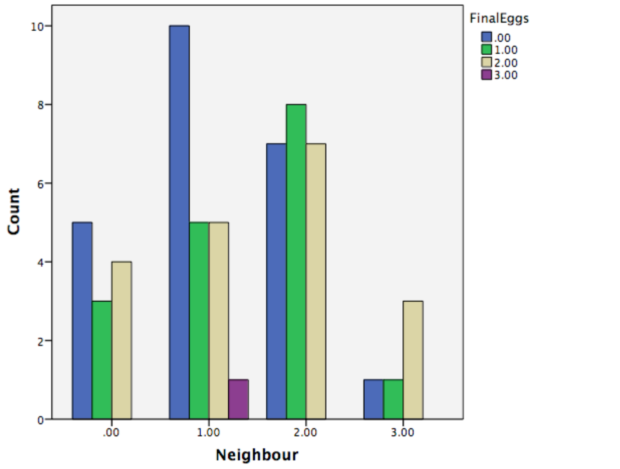

Figure 2: A bar chart displaying the final number of eggs in each neighbour category. There is no statistically significant difference across categories, meaning that final clutch size during this study was evenly distributed across the colony.

Concluding comments

Coulson (2011) reports that the average clutch size for Kittiwakes is just fewer than two eggs, with a slight skew to one-egg clutches. However, he also notes that average clutch size is more stable in some colonies, than others. For example, data collected in North Shields from 1954-1990 gave an average of 2.03 eggs per clutch with little variance, whereas four years of data from a colony in Arctic Russia saw an average of 1.91 eggs with a range of 1.53-2.33. Coulson also notes that as female breeding experience increases so does the ability to replace lost eggs within a season.

The average clutch sizes presented in this paper are smaller than those reported by Coulson from his long-term study. This is possibly a sample size effect. Coulson and Thomas (1985) report sample sizes for clutch size calculations. For birds in the middle range of breeding experience, samples ranged from 80-156. But the overall range, across all breeding experience categories, was from 50-205. I would assume that the colony at Aztec Zawn captures a range of breeding experience. However, as Coulson and Thomas make clear, birds in their first breeding season produced a smaller average clutch size across their entire study (mean=1.88). Even if the Aztec Zawn colony were all inexperienced breeders an average clutch size of fewer than one egg suggests other stresses are in play.

A key stressor may be predation. It is possible that sustained predation will erode colony edges, revealing new edges of nests that were previously better defended. This may increase both the rate and amount of predation, and if this outstrips egg replacement the colony will collapse (I am indebted to the editor, Mike Lock, for raising this possibility). However, this relies upon the new edges being accessible to the predator. My observations above indicate that Great Black-backed Gulls are clumsy and look to find relatively easy access to nest sites. Those Kittiwakes on the more precipitous parts of the colony, irrespective of their proximity to a colony edge, may be better protected. This might explain why the centre of a colony is the choice of the early arrivals. In effect this means there are two edges: the edge of the colony and the edge of the predator's physical landing limit. It would be of great interest to collect precise geometric data for a colony, perhaps using 3-D laser survey techniques to map the terrain outside of the breeding season. This might provide information about the geography of colony structure and its impact upon overall productivity. Some colonies may reside on better and more naturally defended real estate.

It is worth noting that Davis & Jones (2007) discuss the possibility, for auks, that the presence of an apex predator, such as a Great Black-backed Gull deters other gull species, thus, the overall colony losses are reduced. Such an effect may generalize to Kittiwakes. Davis and Jones report that Great Black-backed Gulls on Lundy have recovered their numbers in 2004, to 58 pairs on the island, but more recent data is not available. There is no directly observable relationship between Great Black-backed Gull numbers and the decline in Kittiwake populations on Lundy. Also, other *Laridae* species have declined in breeding numbers on the island, though Corvids appear to thrive. It would be of interest to map Great Black-backed Gull nest sites on the island in order to calculate their proximity to cliff-nesting colonial seabirds, and to relate this to average clutch size and final productivity.

Whilst a Great Black-backed Gull may deter other predators, a small colony may still be vulnerable to failure if its rate of egg replacement falls below that of the needs of the resource-guarding predator. Great Black-backed Gulls are generalist predators and will also scavenge. It is unlikely that they rely on Kittiwake eggs and therefore unlikely that outstripping a colony will reduce available resource. None the less, it would be useful to know the precise role of this resource in the foraging strategies of Great Black-backed Gulls.

Predation is unlikely to be the sole cause of the reduction in breeding Kittiwakes on Lundy but by studying those Kittiwake colonies that do persist we may begin to understand what constitutes resilience in the face of key challenges. To that end the Kittiwakes of Lundy warrant continued study.

Acknowledgements

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References

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