DIFFERENCES IN AGGRESSION AND NEST BEHAVIOUR BETWEEN HERRING GULLS (*LARUS ARGENTATUS*) AND LESSER BLACK-BACKED GULLS (*LARUS FUSCUS*) ON LUNDY

by
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ABSTRACT

Herring gulls (*Larus argentatus*) and Lesser Black-backed gulls (*Larus fuscus*) persist as distinct species by differentially exploiting shared environments. Differences in aggression and nesting behaviour were studied on Lundy using field observations in two neighbouring colonies. No significant differences were found in commission of aggression and nest attendance. In areas bereft of vegetation other nest characteristics mediated visibility of chicks and aggression at the nest. Herring gulls behaved similarly to Lesser Black-backed gulls in this ecology; the results did not indicate that the Herring gull is significantly less well adapted to the offshore ecology of Lundy.

Keywords: *Laridae, nesting, topography, aggression, ecology*

INTRODUCTION

The *Laridae* of seabirds is made up of 50 species that occupy a variety of habitats (Pons, Hassanin & Crochet, 2005). This family includes the gulls, a group whose morphological and behavioural differences are 'neither numerous nor particularly striking' (Tinbergen, 1963, p.210).

Speciation amongst the *Laridae* may have been aided by geographical isolation in the past (Hosey & Goodridge, 1980), but a number of species now nest in mixed or adjacent colonies, including Herring and Lesser Black-backed gulls. The Herring gull (HG; *Larus argentatus*) and Lesser Black-backed gull (LBB; *Larus fuscus*) (Plate 1) increased in numbers in the early part of the last century (Haycock & Threlfall, 1975; Camphuysen, 1995), but are now declining across Britain as a whole, with the HG showing a decrease of 69% in estimated population numbers between 1969 and 2008, and the LBB showing a 7% population decrease between 1986 and 2008 (JNCC, 2009). However, there is considerable regional variation for both species, with populations showing increases at some colonies and decreases at others (Mavor, Heubeck, Schmitt & Parsons, 2006) despite an overall downward trend.

Environmental overlap and a large degree of uniformity in morphology and behaviour, occurring in conjunction with significant reproductive isolation (Hosey & Goodridge, 1980), appears to contradict the 'competitive exclusion principle' (CEP; Hardin, 1960). This principle states that complete competitors cannot coexist (Hardin, 1960), meaning if two largely non-interbreeding populations occupy the same ecological

Herring gull and chick – *Larus argentatus argenteus.*
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Lesser Black-backed gull and chick – *Larus fuscus graellsii.*
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Plate 1: The study species

niche and the same geographic territory, then if one population holds a fitness advantage over the other the second population will, over time, be displaced by the fitter population and possibly go to extinction. It follows that 'ecological differentiation is the necessary condition for coexistence' (Hardin, 1960, p.1296). Following the CEP, a reasonable hypothesis would be that HG and LBB can coexist because they occupy marginally different ecological niches or exploit the same one in different ways.

A way to assess such differences is to measure behaviour. For example, researchers have investigated differences in feeding (Verbeek, 1977b) and nesting behaviour (Calladine, 1997; Hosey & Goodridge, 1980; Burger, 1977). Findings show that LBB and HG have been able to coexist by exploiting overlapping food sources in different ways (Verbeek, 1977a, 1977b) and preferentially utilizing nest sites with different topographical features (Calladine, 1997; Garthe, Freyer, Huppop & Wolke, 1999), allowing them to exploit subtly different ecologies within the same overall environment.

Verbeek (1977a), studying a mixed colony of HG and LBB on Walney Island, Cumbria, UK argued that different foraging strategies between these species are the consequence of divergent evolutionary pathways, with the LBB being more migratory and pelagic than the HG. This has resulted in the LBB being smaller, tending to forage on the open sea and travel further in search of food (Verbeek, 1977b).

Calladine (1997) reported similar differences in foraging behaviour that seem to result from the species' different evolutionary trajectories, with LBB travelling out to the open sea and HG exploiting inshore food sources on the intertidal zone. This neritic tendency of the HG, perhaps being a result of their more resident evolutionary past (Liebers *et al.* 2004), has resulted in their foraging behaviour being greatly influenced by the tides (Garthe *et al.* 1999).

Nesting behaviour has also received attention. Calladine (1997), studying a mixed breeding colony on the Isle of May, East Scotland, extended an analysis of differences in foraging behaviour to examine the impact of foraging on nesting behaviour. He assessed that, amongst LBB, travelling further to forage resulted in less time spent at the nest by adults and this directly influenced nest site selection. Calladine (1997) attributed an LBB preference for nesting in areas of long vegetation to their pelagic foraging behaviour, arguing that vegetation around the nest site facilitates concealment of chicks during parental absence on foraging bouts.

Further research (Burger, 1977) has assessed the differences in selected nest sites and their potential adaptive consequences. Discussing the LBB preference for nesting at vegetated sites, Burger (1977) reported that the presence of barriers created by vegetation reduces aggression between colony members. Hosey and Goodridge (1980), when studying similar variables of nesting topography, suggested that reduced aggression due to the presence of nest site vegetation may result in greater reproductive success for LBB in comparison to HG. The assumptions contained within the previous research literature described above are summarised in Table 1.

Research reported in this paper tested assumptions 5-10, 14 and 15 in Table 1 using adjacent HG and LBB colonies on Lundy, a granite rock island in the outer Bristol Channel. At its closest point to the UK mainland the island is approximately eleven miles from the Devon coast. Due to its distance from the mainland, and limited access to anthropogenic food sources, Lundy can be considered as having a more offshore ecology than previous study sites (Verbeek, 1977a, 1977b; Burger, 1977; Hosey & Goodridge, 1980).

Species	Behaviour	Assumption	Research
Lesser Black-backed gull	Foraging	1. Pelagic – travels out to forage on open sea	Verbeek (1977b); Calladine (1997); Garthe, Freyer, Huppop & Wolke (1999)
		2. More manoeuvrable	Verbeek (1977b)
	Nesting	3. Nests in long vegetation	Calladine (1997)
		4. Individual defence during incubation	Calladine (1997)
		5. Greater parental absence from nest during chick rearing phase	Calladine (1997)
		6. Greater concealment of chicks	Calladine (1997)
		7. Vegetation reduces aggressive encounters	Burger (1977)
		8. Long vegetation may mean greater fitness	Hosey & Goodridge (1980)
Herring gull	Foraging	9. Neritic – forages on intertidal zone	Verbeek (1977b)
		10. Foraging influenced by tide levels	Garthe, Freyer, Huppop & Wolke (1999)
	Nesting	11. Nests on rocky areas	Burger (1977); Hosey & Goodridge (1980)
		12. Greater spacing of nests	Hosey & Goodridge (1980)
		13. More aggression within HG colony due to lack of barriers to visibility of neighbours	Hosey & Goodridge (1980); Burger (1977)
		14. Greater chick visibility at nest site due to lack of barriers to visibility	Calladine (1997); Burger (1977); Hosey & Goodridge (1980)
		15. Greater parental nest attendance and vigilance due to increased chick visibility	Calladine (1997)

Table 1: Lesser Black-backed gulls and Herring gulls behavioural differences

LBB populations return to Lundy between February and April, after overwintering in Southern Europe and North Africa, and nest largely in breeding colonies on the slopes of long grass on the west coast of the island before migrating south again by September. Survey data from the 1950s to the 1990s showed a steady increase in numbers of nesting LBB on Lundy. Since the 1990s LBB populations increased substantially on Lundy with the population estimated between 400 and 500 breeding pairs (Davis & Jones, 2007). The LBB populations on Lundy represent the majority of Devon's population of breeding LBB (Davis & Jones, 2007). Like the LBB, the majority of HG on Lundy nest on the west coast. This species nests mainly on broken cliffs of granite boulders. They return to the island in late winter to breed and, despite being less migratory than LBB, most leave again in September. The HG population on Lundy has declined significantly since the 1960s, in part due to control measures to prevent predation of auks, but surveys since the 1990s show a more stable population of between 700 and 800 nesting pairs (Davis & Jones, 2007).

Following Verbeek (1977b), who noted that gull species engage in conspecific predation and kleptoparasitic behaviour in food-stressed environments, we measured the frequency of aggressive behaviours committed by both species as an assay of differential food stress that would indicate if one of the species was having greater difficulty in meeting its energy demands on Lundy. We were principally interested in encroachment aggression, where a territorial boundary was transgressed. Territorial behaviour in ground-nesting gulls is principally defence of reproductive investment. We have assumed that threat from

conspecific predation is not a constant but rather variable. Moreover, we have assumed that the costs for the aggressor of possible injury are outweighed by the nutritional and caloric benefit under food stress of a predated chick. Therefore, food stress is a key independent variable in our background theoretical model.

We measured nest attendance to see whether either species spent longer at the nest. This was viewed as an index of the effectiveness of the different foraging strategies typical of each species (Table 1) and of risk, as the longer chicks are left unattended the more vulnerable they are to predation. Additionally, the preferred nesting substrates of each species (Table 1) were assessed to see if these characteristics had any moderating effect on the frequency of aggression experienced at the nest and how well chicks were concealed. Thus we are assuming a trade-off between time spent foraging and increasing risk of chick mortality from conspecific and other predation. Under food stress, and where other strategies such as conspecific predation are limited by counter measures and a finite limit of available chicks, we would expect adults to increase their foraging time to resource their chicks.

To summarise, we hypothesised that behavioural differences have allowed LBB and HG to avoid direct competition and coexist as separate species. These behavioural differences will have different costs and payoffs across environments. Previous studies have used inshore/mainland nesting locations. This study adds to these accounts by using a coastal site. It is possible that HG and/or LBB experience different costs in this environment which in turn will enable researchers to determine which ecology these gulls are best adapted to. The focal costs for this study are a greater nest absence and an increase in aggression.

METHODS
Study Site and Subjects
Colony Site
Two gull colonies were situated directly south of Battery Point on the west coast of Lundy. Observations took place between 23 June and 5 July 2011 (Plate 2). These colonies were situated adjacent to one another but separated by geographical features. Plate 3 shows a photograph of the locations of the two colonies relative to one another.

The first colony, designated Battery Upper, was situated on an inclined bank leading down to a cliff edge. The lower boundary of the colony was marked by this interface between the inclined bank and cliffs which dropped away vertically for approximately two hundred feet to the Atlantic below. This colony consisted of about 50-60 nests.

Hourly head counts of LBB and HG in the colony were conducted throughout the study period and LBB:HG ratios computed. These showed LBB:HG ratios ranging from 2-11 LBB: 1 HG. These head counts did not discriminate between colony members and birds 'visiting' the colony, so all visible birds were counted including those just loafing at the site. Those nesting in the colony were almost entirely LBB, so Battery Upper was deemed to be a LBB colony.

The topography of Battery Upper was a mixture of flat terrain, broken in places by granite boulders. The colony was vegetated with patches of short grass (Order: *Paoceae*) interspersed among areas of taller vegetation including thrift *(Armeria maritima)* and bracken *(Pteridium aquilinum)*. Along with the granite boulders, the bracken provided considerable cover for nest sites and contributed to the broken aspects of the terrain (Plate 3).

Plate 2: Lundy Island showing the location of study colonies marked with star. (Map of Lundy Island, n.d.)

Battery Upper
Observation Position

North

Battery Lower
Observation Position

Battery Lower colony
(circled)

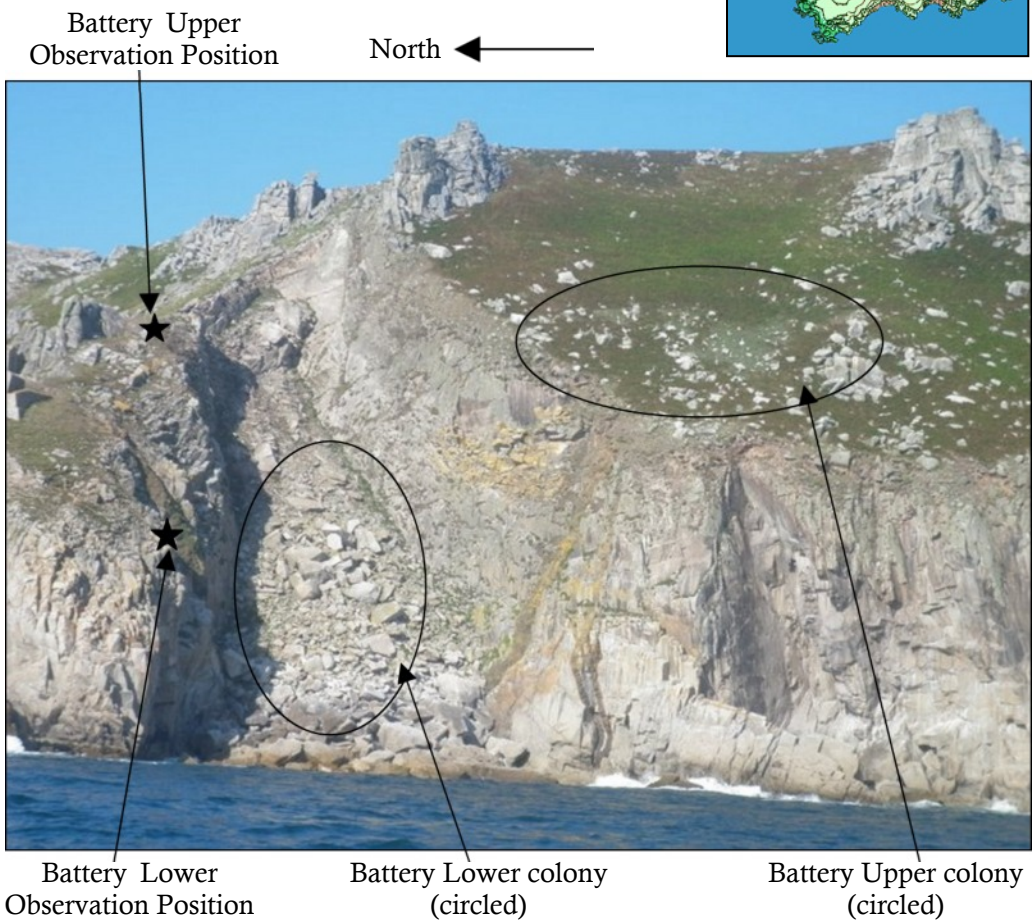Battery Upper colony
(circled)

Plate 3: Battery Upper and Battery Lower colonies and their respective observation positions. Photo © Kirsty Neller – reprinted with permission

The second colony, designated Battery Lower, was situated in a stone-chute at the foot of cliffs that marked the north boundary of Battery Upper colony. The two colonies were adjacent to one another but separated by a two hundred foot difference in elevation. The north boundary of Battery Lower was marked by another cliff face, again with cliffs up to two hundred feet high, on top of which are the remains of the old Battery.

Battery Lower colony was situated on granite rocks leading down to sea level on the lower boundary. As already indicated, the north and south boundaries of Battery Lower were marked by sheer cliffs that sheltered the colony in its own inlet. Battery Lower consisted of in excess of fifty nests, which were almost entirely HG. Hourly head counts throughout the study period showed HG:LBB ratios ranging from 5-52 HG: 1 LBB; again, these counts didn't differentiate between nesting birds and those loafing around the colony. Battery Lower was deemed to be a HG colony. Topographically, Battery Lower consisted of a highly broken terrain of granite boulders and was almost entirely bereft of vegetation (Plate 3).

Nest Characteristics

Burger (1980) defined the traits of 'nests' for ground-nesting gull species. The area padded with nesting material by the adult, where the clutch is incubated, is the 'unique territory'. The immediate area surrounding this is controlled by the nesting adult pair, and is the 'primary territory'. The 'unique' and 'primary' territory boundaries in the current study were determined, during preliminary observations conducted between 24/06/11 and 27/06/11. The boundary of the primary territory was judged by the frequency of aggressive territorial clashes and displacement behaviours. As the colonies were already established and the density of nests stable, the boundaries of these micro-territories were relatively fixed. The size of primary territories was influenced by the density of nests and the terrain of the colonies, but generally covered an irregular shaped area of up to two metres around the unique territory. Plate 4 shows primary territories for nests in a section of Battery Lower.

Plate 4: Annotated photograph showing primary territories (circled) for nests in Battery Lower colony. Photo © Robert Spencer

After Calladine (1997), the following nest site features were assessed within the primary territory: position of the nest within the colony, dichotomised as centre or edge; vantage points, defined as features an adult gull could use to keep look-out over its nest, classified as present or absent; topography, used to describe the ground at the nest as either 'broken', where boulders and rocks create a heavily contoured environment restricting visibility and movement, or 'flat', where terrain was fairly level.

The locations of nests were categorised as 'hidden' or 'exposed'. A hidden nest was defined as a nest that, when viewed from each of the four compass points, could not be seen from at least two of these viewpoints, assessed at two heights for each point – the first from a metre away at 30-40cm from the ground, the height of an adult gull (Pierotti, 1982); the second from about a metre away at the height of a standing adult human of between 5 feet and 6 feet tall. The level of vegetation around the nest was categorised as constituting 'nil', 'less than one-third', 'one-third to two-thirds' or 'over two-thirds' of the primary territory (Calladine, 1997).

Eleven study nests (n=11) were identified. These were five LBB nests and one HG nest in Battery Upper and five HG nests in Battery Lower. The number of chicks on each nest as well as the characteristics of each nest were described and defined during the period of preliminary observations (Table 2).

Nest	Species	Chicks	Position	Vantage	Topography	Location	Vegetation
BU1	LBB	2	Centre	Present	Flat	Exposed	$^2/_3$+
BU2	LBB	2	Centre	Present	Flat	Exposed	$^2/_3$+
BU3	LBB	2 *	Centre	Absent	Flat	Exposed	$^1/_3$ - $^2/_3$
BU4	LBB	1	Edge	Absent	Broken	Hidden	$^2/_3$+
BU5	LBB	1	Edge	Absent	Broken	Hidden	$^2/_3$+
BU6	HG	1	Edge	Absent	Flat	Hidden	$^1/_3$ - $^2/_3$
BL1	HG	1	Centre	Present	Broken	Exposed	Nil
BL2	HG	1	Centre	Present	Broken	Exposed	Nil
BL3	HG	1	Centre	Present	Broken	Exposed	Nil
BL4	HG	1	Edge	Present	Broken	Hidden	Nil
BL5	HG	1	Edge	Present	Broken	Hidden	< $^1/_3$

Key
Nest: BU = Battery Upper. BL = Battery Lower.
Species: LBB = Lesser Black-backed gull. HG = Herring gull.
Chicks: Number of hatchlings/nest.
Position: Position of nest within colony - Centre or Edge.
Vantage points: Present or absent.
Topography: Ground in immediate surroundings is, either, broken by environmental features and difficult to move around on, or flat and gulls can walk around the area with relative ease.
Location: Is actual nest exposed or hidden.
Vegetation: Level of vegetation in nest micro-territory. Nil, < $^1/_3$; $^1/_3$ - $^2/_3$; $^2/_3$+

* The initial 2 chicks shown for nest BU3 was reduced to 1 following one of the chicks being predated by a Herring gull on 28/06/11. This occurred during a break from observations so,unfortunately, no data was being recorded at the time of the predation despite being witnessed by observers.

Table 2: Study nest characteristics

Behavioural measures

Behavioural observations of parental nest attendance, chick visibility and aggressive encroachments were recorded for each nest between 28/06/11 and 05/07/11. The colonies were already established and nesting gulls had completed the laying and incubation stages. Nesting birds had chicks on the nest of varying ages that had not yet fledged.

Parental nest attendance and chick visibility were recorded at five-minute scan samples. The recording rule used was instantaneous sampling (Martin & Bateson, 2007). The five minute time interval was chosen following preliminary observations as this allowed data on nest attendance and chick visibility to be recorded effectively without detracting from the recording of all occurrences of aggressive encroachments. Data on aggressive encroachments was recorded continuously as frequency counts per nest.

Weather conditions and tide levels were also recorded. Wind speed was measured by observers' approximations using the Beaufort Wind Scale (Met Office, n.d.). Tide levels were assessed on a six- to six-and-a-half-hour tidal cycle, with a two-hour period either side of high tide being classed as high tide levels, and correspondingly two-hour periods either side of low tide were classed as low tide levels.

Procedure

Observations were conducted on the two colonies simultaneously and at different times during the hours of daylight over the study period. Plate 3 shows the observation positions used. There were two observers for each colony. This ensured that one observer could maintain observation of all nests whilst the other recorded the data. Observers switched colonies at two-hour intervals and interchanged observer pairings on consecutive days of the study to provide some control for inter-observer reliability. The effectiveness of this control was not measured statistically but was monitored through concurrence on head and ratio counts. Observers showed a large degree of agreement, with head counts frequently matching or being within a few counts of each other and giving essentially the same ratios.

Thirty-four hours of observational data were recorded for nests 1 to 5 in Battery Upper and twenty-nine hours for Battery Upper nest 6 (added on the second day of data collection – 29/06/11). Thirty-five hours of data were recorded for Battery Lower, giving, with the exception of nest 6 in Battery Upper, a total of sixty-nine hours of data for both colonies.

Analyses

The data collected for all variables was explored to test for normality and homogeneity of variance. Kolmogorov-Smirnov and Shapiro-Wilk tests of normality and Levene's test for homogeneity of variance indicated that much of the data was significantly non-normally distributed and also violated the assumption of homogeneity. These factors in conjunction with the small sample sizes meant the decision was taken to use non-parametric statistical tests for all statistical analyses.

Frequency counts of aggressive encroachments committed at each nest and the species of aggressor, either HG or LBB, permitted a comparison of amount of aggression committed by each species at the study nests using Mann-Whitney U test.

This was taken as a general assay of the overall level of aggression for that species in the Lundy environment.

Tide levels were generalised into three categories (Low/Mid/High) and data on HG and LBB nest absence was analysed as frequency of occasions both of the nesting pair were absent from the nest. Friedman's ANOVA and post hoc Wilcoxon signed rank test were used to assess, within species, if there were significant patterns of nest absence for either species at different tide levels. A species comparison of nest absence was also conducted to assess any significant difference between species at the three different tide levels. Due to the lack of a non-parametric version of a mixed design ANOVA statistical test, a species comparison was conducted separately at each tide level using Mann-Whitney U test.

An assessment of the overall level of nest attendance for each species was also conducted by comparing HG and LBB on three levels of possible nest attendance: 'absent from the nest' - when both adults were away from the nest simultaneously, 'one adult present' – number of sampled occasions one adult was present at the nest, and 'two adults present' – number of occasions when both adults were present at the nest. Again, due to the lack of an effective non-parametric mixed design statistical test, Mann-Whitney U test was used to compare the species at each level of nest attendance separately.

An assessment of the five categories of nest site characteristic (Position, Vantage Points, Topography, Location and Vegetation) was contingent on the premise that high levels of aggression occurring at the nest and highly visible chicks are factors that can be used to assay the costs of chosen nests sites. To analyse this, first, we used a bivariate linear correlation analysis on the two factors, aggressive encroachments and chick concealment, across all study nests to see if these measures co-vary in any significant way.

Second, an analysis of differences in chick visibility between the species was conducted by comparing data for average chick visibility between HG and LBB nests. The conversion of chick visibility data to a percentage score was conducted due to variation in the number of chicks between nests, percentage scores thereby allowing the statement of a ratio of amount of time chicks were visible to amount of time concealed for each species. A species comparison of chick visibility was then conducted using Mann-Whitney U test.

Third, an analysis of the influence of vegetation level on frequency of aggressive encroachments and how well chicks were concealed was conducted. For both aggressive encroachments and chick concealment the Kruskall-Wallis test for independent groups was used followed by post hoc comparisons using Mann-Whitney U test. Jonckheere's test was then used to assess any trends in the data.

Last, the influence of the other categories of nest site characteristic (Location, Vantage Points, Topography, Position) on aggressive encroachments and chick concealment was analysed. As these were dichotomised variables Mann-Whitney U test was conducted for all analyses using frequency counts for aggression and chick concealment scores.

RESULTS
The results of all statistical analyses are presented in Tables 3, 4 and 5.

Analysis	Sample Size	Median	Test Statistic	Post hoc	p-value	Units (frequency counts)
Species differences in aggression	22	HG=24.00 LBB=4.00	U=40.00		p=0.09	HG=388 LBB=366
Species differences in nest attendance						
Absent	11	HG=24.50 LBB=22.00	U=10.5		p=0.18	HG=606 LBB=403
1 adult	11	HG=55.00 LBB=61.00	U=14.50		p=0.48	HG=1360 LBB=1146
2 adults	11	HG=21.00 LBB=26.00	U=12.50		p=0.35	HG=482 LBB=491
Tidal influences on nest absence						
HG	48		$X^2(2)=6.1$		p=0.047	Low - 258 Mid - 259 High - 89
Low-Mid Tide	65	Low=2.00 Mid=2.00		T=480	p=0.13*	
Low-High Tide	48	Low=2.00 High=0		T=208	p=0.01*	
Mid-High Tide	48	Mid=2.00 High=0		T=220.50	p=0.001*	
LBB	40		$X^2(2)=8.48$		p=0.014	Low - 183 Mid - 165 High - 55
Low-Mid Tide	65	Low=2.00 Mid=2.00		T=649	p=0.36*	
Low-High Tide	40	Low=2.00 High=1.00		T=86.50	p<0.001*	
Mid-High Tide	40	Mid=2.00 High=1.00		T=195	p=0.024*	
Species Comparison						
Low Tide	155	HG=2.50 LBB=2.00	U=2817		p=0.35	HG - 258 LBB - 183
Mid Tide	131	HG=3.50 LBB=2.00	U=1944.50		p=0.17	HG - 259 LBB - 165
High Tide	88	HG=0 LBB=1.00	U=897.50		p=0.29	HG - 89 LBB - 55

* Bonferroni correction applied, associated significance level adjusted to 0.0167

Table 3: Results of analyses for aggression, nest attendance and tidal nest absence

Tidal influences on nest absence

Significant results were detected for tidal influences on nest absence for both species. Nest absence in HG differed significantly with tide level (Freq: HG: Low=258, Mid=259, High=89), $X^2(2)=6.1$, p=0.047. Post hoc tests using Wilcoxon signed rank test were used to assess between which tide level conditions the significant differences

lay (Bonferroni correction applied, associated significance level (asl): 0.0167). HG absence from the nest was significantly different between Low tide (Mdn=2.00) and High tide (Mdn=0), T=208, p=0.010, r=-0.34. Absence from the nest was also significantly higher at Mid tide (Mdn=2.00) than at High tide (Mdn=0), T=220.50, p=0.001, r=-0.44. HG on Lundy were significantly more likely to be away from their nests at Low and Mid than at High tide.

For LBB, Friedman's ANOVA indicated a significant difference in nest absence at different tide levels (Freq: LBB: Low=183, Mid=165, High=55), X²(2)=8.48, p=0.014. Post hoc tests using Wilcoxon signed rank test (Bonferroni applied, asl: 0.0167) showed a significant difference between Low tide (Mdn=2.00) and High tide (Mdn=1.00), T=86.50, p<0.001, r=-0.53, indicating LBB were significantly more likely to be away from their nest at Low tide than at High tide. Comparisons of differences between the species did not detect a significant difference between LBB and HG at any tide level (See Table 3 and Figure 1).
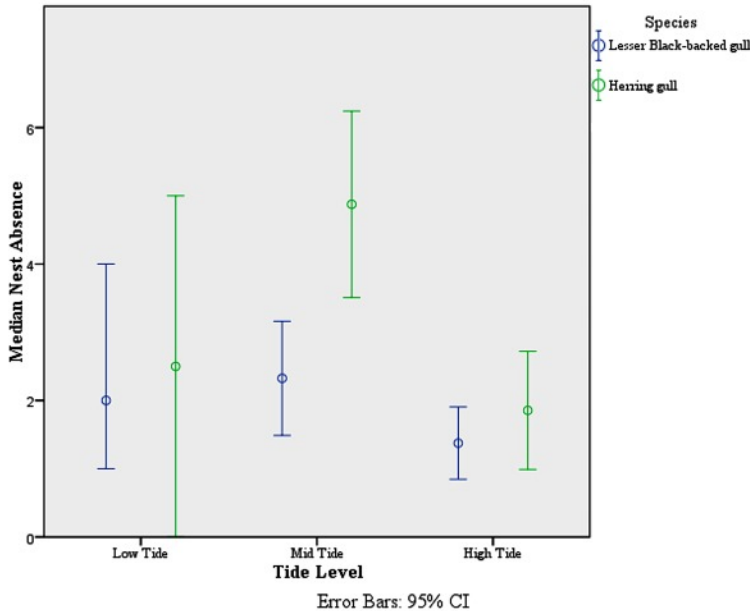

Figure 1: Species comparison of tidal nest absence

Correlation between chick concealment and frequency of aggressive encroachments
A bivariate linear correlation analysis conducted on frequency of aggressive encroachments and number of times 'Nil' chicks were visible at the nest, being taken as an assay of chick concealment, showed a significant negative linear relationship between chick concealment and amount of aggressive encroachments occurring at the nest, r=-0.64, p(one-tailed)=0.02. This indicated that at nests where chicks were better concealed fewer aggressive encroachments occurred as shown in Figure 2.

Influence of level of vegetation on aggressive encroachments and chick concealment
Aggressive encroachments: Kruskal Wallis test for comparing independent groups showed the frequency of aggressive interactions at the nest was significantly affected by
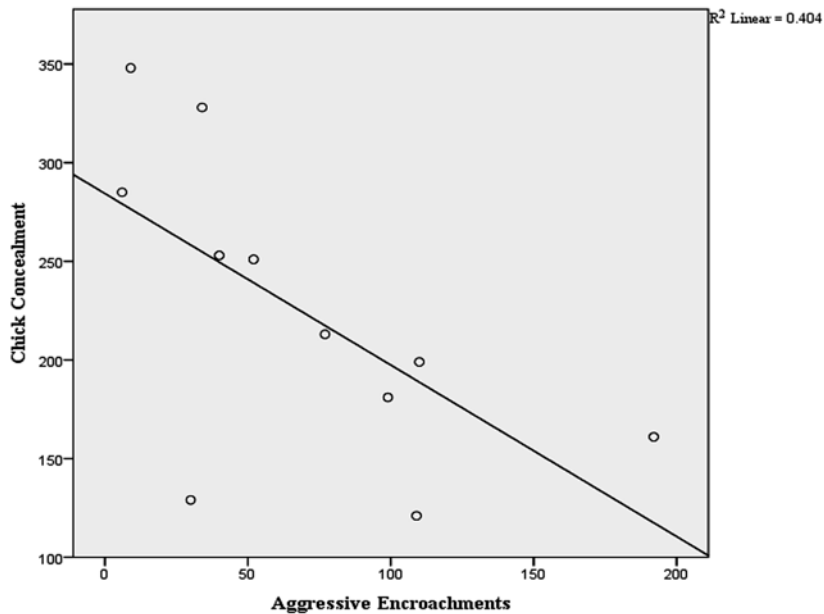
Figure 2: Correlation between aggressive encroachments and chick concealment

the level of vegetation at the nest site (Freq: Nil=300, $<1/3$ =30, $1/3$-$2/3$=144, $2/3$+=284), H(3)=15.96, p=0.001. Three post hoc comparisons using Mann-Whitney U tests were conducted to follow up this finding (Bonferroni applied, asl: 0.0167).

Comparisons showed frequency of aggression was significantly higher at nests with 'Nil vegetation' (Mdn=1.00) than at nests with 'Less than $1/3$ vegetation' (Mdn=0), U=1687, z=-2.97, p=0.001, r=-0.22. However, the effect size for this difference was small and may have been due to the category of 'Less than $1/3$ vegetation' containing only one nest and therefore the fewest number of samples (n=35) rather than any beneficial characteristic of this level of vegetation cover.

Jonckheere's test was used to test for trends between increasing vegetation and decreasing aggression and showed a pattern of descending medians that was not statistically significant, J=23115, z=-0.94, r=-0.05 (Table 4).

Chick concealment: Chick concealment was significantly affected by level of vegetation at the nest (Freq: Nil=806, $<1/3$=129, $1/3$-$2/3$=527, $2/3$+=1007), as assessed by Kruskall-Wallis test for independent groups, H(3)=32.48, p<0.001. Post hoc comparisons using Mann-Whitney U test (Bonferroni applied, asl: 0.0167) showed a significant difference between nests with 'Nil' (Mdn=6.00) and '$1/3$ - $2/3$' vegetation (Mdn=10.00) with chicks being significantly better concealed at nests with '$1/3$ - $2/3$' vegetation, U=2963.50, z=-3.77, p<0.001, r=-0.26.

The comparison between nests with 'Nil' (Mdn=6.00) and '$1/3$ -$2/3$' vegetation (Mdn= 10.00) showed that chicks were significantly better concealed at nests with '$1/3$-$2/3$'vegetation, U=2963.50, z=-3.77, p<0.001, r=-0.26. A comparison between nests with 'Nil' (Mdn=6.00) and 'Greater than $2/3$' vegetation cover (Mdn=8.00) showed higher levels of chick concealment at nests with more vegetation. This result was also significant, U=7569, z=-2.99, p=0.003.

The finding that vegetation is a factor influencing how well chicks are concealed was confirmed using Jonckheere's test, J=28271.50, z=3.64, r=0.05, which showed a pattern of ascending medians indicating that as vegetation level increased chick concealment also increased (Table 4).

Analysis	Sample Size	Median	Test Statistic	Post hoc	p-value	Units
Correlation between chick concealment and aggression	11		r=-0.64		p (one tailed) =0.02	Agg=758 Chick conceal=2469
Species differences in chick visibility	11	HG=48.50 LBB=48.00	U=12		p=0.32	HG=47% LBB=41% ‡
Influence of vegetation on aggressive encroachments	Total: 374 Nil: 140 <1/3 : 35 1/3-2/3 : 63 2/3+: 136		H(3)= 15.96		p=0.001	Nil=300 <1/3 =30 1/3-2/3 =144 2/3+=284 †
Nil - < 1/3 Vegetation	175	Nil=1.00 < 1/3 =0		U=1687	p=0.001*	
Nil - 1/3- 2/3	203	Nil=1.00 1/3-2/3 =1.00		U=3865	p=0.08*	
Nil - 2/3+	276	Nil=1.00 2/3+ =1.00		U=8644	p=0.08*	
Aggression trends across levels of vegetation	374			J=23115	p=0.174	
Influence of vegetation on chick concealment	Total: 374 Nil: 140 <1/3 : 35 1/3-2/3 : 63 2/3+: 136		H(3)= 32.48		p<0.001	Nil=806 <1/3 =129 1/3-2/3 =527 2/3+=1007 †
Nil - < 1/3 Vegetation	175	Nil=6.00 < 1/3 =3.00		U=1917	p=0.045*	
Nil - 1/3- 2/3	203	Nil=6.00 1/3-2/3 =10.00		U=2963.50	p<0.001*	
Nil - 2/3+	276	Nil=1.00 2/3+ =1.00		U=7569	p=0.003*	
Chick concealment trends	374			J=28271	p<0.001	

†=Units shown are frequency counts. ‡=Units shown are percentages
*=Bonferroni correction applied, associated significance level adjusted to 0.0167

Table 4: Influence of vegetation on chick concealment and aggression

Analysis	Sample Size	Median	Test Statistic	Units (frequency counts)	p-value
Influence of nest characteristics on aggression					
Vantage Points	11	Present=77 Absent=21.50	U=7.00	Present=599 Absent=159	p=0.23
Topography	11	Broken=40 Flat=93.50	U=6.00	Broken=345 Flat=413	p=0.16
Location	11	Hidden=30 Exposed=104	U=0	Hidden=119 Exposed=639	p=0.004
Position	11	Centre=104 Edge=30	U=0	Centre=639 Edge=119	p=0.004
Influence of nest characteristics on chick concealment					
Vantage Points	11	Present=181 Absent=306.50	U=3.00	Present=1309 Absent=1160	p=0.04
Topography	11	Broken=251 Flat=206	U=14.00	Broken=1568 Flat=901	p=1.00
Location	11	Hidden=285 Exposed=190	U=5.00	Hidden=1343 Exposed=1126	p=0.08
Position	11	Centre=190 Edge=285	U=5.00	Centre=1126 Edge=1343	p=0.08

Table 5: Influence of nest characteristics on aggression and chick concealment

Influence of other nest site characteristics on aggression and chick concealment
Aggressive encroachments: Four categories of nest site characteristic were assessed to see if these features significantly influenced the amount of aggression experienced at the nest ('Location', 'Vantage Points', 'Topography' and 'Position'). Mann-Whitney U tests were conducted on aggression data for each category. Statistically significant results were detected for 'Location' and 'Position' (Table 5).

'Location' categorised nests as 'Hidden' (Freq: 119) or 'Exposed' (Freq: 639). Hidden nests (Mdn=30.00) experienced less aggressive encroachments than exposed nests (Mdn=104.00), and this difference was significant, U=0, z=-2.74, p=0.004, showing a large effect size, r=-0.83, indicating that about 69% of the variance in aggression between the groups was due to whether the location of the nest was hidden or exposed (Figure 3).

The 'Position' of the nest in the 'Centre' (Freq: 639) or at the 'Edge' (Freq: 119) of the colony showed that nests at the centre (Mdn=104.00) experienced more aggression than nests at the edge (Mdn=30.00). This difference was statistically significant, U=0, z=-2.74, p=0.004, r=-0.83, indicating a large amount of variance in aggression (r^2=0.69) between nests could be linked to whether the nest was located on the edge or in the centre of the colonies (Figure 4).
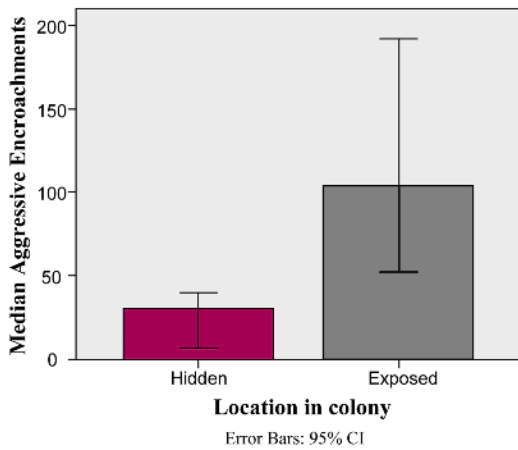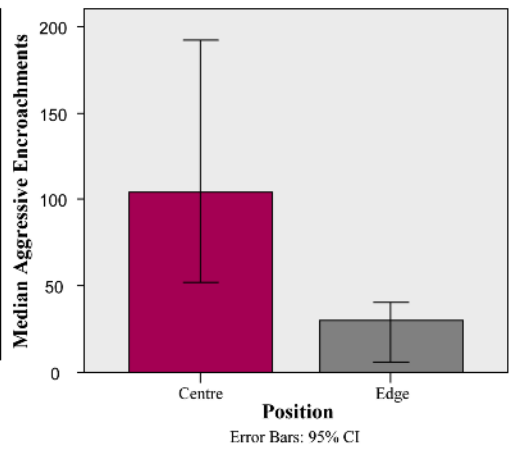
Figure 3: The influence of nest location on aggression

Figure 4: The influence of nest position on aggression

Chick concealment: Mann-Whitney U tests were used to assess the effects on chick concealment of the four categories of nest characteristic ('Location', 'Vantage Points', 'Topography' and 'Position'). The influence of 'Vantage Points' (Burger, 1980) on chick concealment showed that nest sites where vantage points were 'Absent' (Freq: 11160, Mdn=306.50) from the primary territory had better concealed chicks than nests where vantage points were 'Present' (Freq: 1309, Mdn=181.00). This difference was statistically significant, U=3, z=-2.08, p=0.04, r=-0.63 (Figure 5).
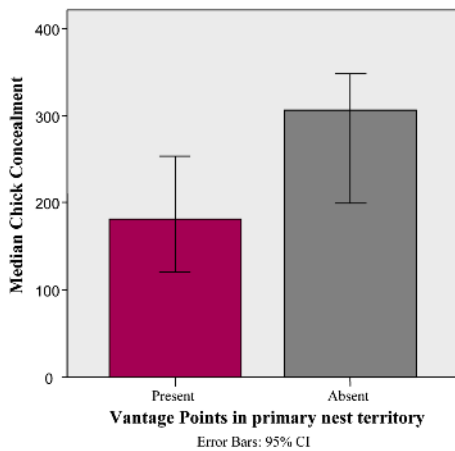

Figure 5: The influence of Vantage Points on chick concealment

DISCUSSION

Species differences in aggression on Lundy

There were no significant differences in aggression between HG and LBB (Freq: HG: 388; LBB: 366) during the current study. We argued that a relatively more difficult feeding ecology, in terms of greater difficulty in meeting daily energy demands, would result in a strategic increase in aggression for either species and we saw this as an assay of food stress. Not all would agree with our initial assumptions. For example, Brown (1967) has argued that aggressive behaviours, such as conspecific predation, are an

extension of the normal hunting behaviour of gulls and not evidence of failing food supply. However, if Brown is correct a more sophisticated model would have to take into account the costs and benefits of prey selection and conspecific predation may only be favourable under certain circumstances.

Tidal influences on nest absence

HG were significantly more likely to be absent from the nest at Low tide and Mid tide than at High tide. This was in line with previous research findings that Low tide is an important foraging window of opportunity for HG as they exploit the intertidal zone for their food sources.

LBB also showed a tidal effect being significantly more likely to be absent from the nest at Low tide than at High tide. Comparisons of tidal nest absence did not show a statistically significant difference between the two species.

These results are in accord with previous research (Verbeek, 1977a, 1977b; Garthe *et al.* 1999) that suggests HG foraging behaviour is heavily influenced by the tide. They also showed a significant amount of nest absence in HG at Mid tide. Mid tide was defined as the two hour period either side of Low tide. This might be a result of Herring gulls having to travel further to reach preferred or suitable foraging grounds due to the lack of a significant intertidal zone for them to exploit on Lundy Island. This is in accord with Verbeek's (1977a) claim that HG will spend more time out of the colony when their preferred food source is not available, such as at neap tide when low tide mussel beds do not get exposed, as they have to travel further to forage. This extension of nest absence, in the current study, across two tide levels and its associated additional energy costs may be an indication that Lundy presents additional feeding challenges to the HG population due to lack of preferred foraging locations.

The tidal effect for LBB is also in accord with previous research. Verbeek (1977a) found on the Walney Island refuse tip that the numbers of both species varied with the tide. Although less pronounced than in the HG, the LBB also appears to exploit Low tide to acquire food. Exactly what it is about this tide level that makes LBB food sources easier to exploit remains unclear. However, it has been noted that despite apparently lacking the behavioural traits found in HG, such as digging (Verbeek, 1977b), the LBB will make use of Low tide food sources. The taking of Rayed trough shells *(Mactra corallina)* from sandbanks at Low tide is a notable example (Verbeek, 1977a).

The results showed both species are reacting to the tide in a similar way and no firm evidence was found that HG are under greater stress in this environment than LBB. Future research on tidal influences on nest absence may benefit from exploring whether the influence of the tide varies across different parts of the nesting season, such as when incubation demands are greatest (Calladine, 1997). It is also possible that there are behavioural differences in low tide exploitation that either rely on the effects of the tide going out and leaving stranded food sources or upon skills of searching for and extracting resource.

The fitness implications of nest characteristics

A significant negative correlation (r=-0.64) between number of times 'nil' chicks were visible and frequency of aggression indicated that at nests where chicks were better

concealed fewer aggressive encroachments occurred. This suggests that a good deal of the aggression occurring in the colonies may have been attempts to defend against chick predation as opposed to territorial disputes between neighbours.

A comparison of HG and LBB nests showed chicks at LBB nests were not significantly better concealed than HG chicks. There were differences in level of vegetation at nests both within and between species, although the general trend was that there was more vegetation at LBB nests. An assessment of the effect of vegetation across all study nests showed that there was no significant trend of decreasing aggression across nests with increasing vegetation. However, an analysis of chick concealment and level of vegetation showed that the more vegetation there was at a nest the better concealed the chicks were.

Other nest characteristics made up the second part of this analysis. For aggression, significant results were found for 'Location' and 'Position', with 'Hidden' nests (Location) and nests at the 'Edge' (Position) of the colonies experiencing less aggression. An assessment of chick concealment indicated that nests where 'Vantage Points' were 'Absent' had significantly better concealed chicks.

The finding that hidden nests experienced less aggression seems intuitively plausible. However, this does provide information about what characteristics are important in mediating aggression at the nest site. A nest could meet the criteria of 'Hidden' in a number of ways including level of vegetation or concealment by rocks and boulders. Hosey and Goodridge (1980) argued that vegetation at Walney Island might have been the only or crucial factor aiding nest concealment. This was not the case on Lundy as rocks and boulders in the colonies performed a similar function.

There was significantly less aggression at nests on the 'Edge' of the colonies. Previous research has suggested that being located at the edge of a colony or group increases predation risk (Stankowich, 2003; Martinez-Abrain *et al.* 2003). For a predator, nests on the edge of a colony are possibly the first and easiest to approach whilst avoiding anti-predator behaviours such as mobbing. This may be particularly true where the colony is located on open and flat land and where the risk from ground predators is chronic. In contrast to this, the absence of ground predators and the position of the colonies on sloping granite cliffs on Lundy may explain the reversal of findings in this research. Alternatively, higher levels of aggression may be the result of increased proximity of neighbours, which might be an inevitable trade-off for increased vigilance at the centre of a colony, whereas peripheral birds are less crowded and fewer neighbours may mean fewer disputes. No data was recorded on nest spacing or nearest neighbour distances for comparison across areas of the colonies but this may be a fruitful avenue for future research.

The third nest characteristic that produced a significant result was the connection between absence of vantage points and high levels of chick concealment. Calladine (1997) has argued that predation can be reduced by selecting a nest site with characteristics that allow the adult to defend the nest or conceal the young. The choice of nest site is likely to be a trade-off between these two factors based on the risks found in that particular nesting environment. For example, if parental defence was the dominant factor, a nest with characteristics that permit increased vigilance and surveillance of the nest would be essential. In contrast, if the overriding factor was chick concealment then the presence of hiding places would be of greater importance. The

relationship between absence of vantage points acting as platforms to defend a territory and high levels of chick concealment may provide support for this line of reasoning. It may also be the case that vantage points act as markers or focal points which can draw attention to the location of the nest.

Concluding comments

A number of avenues of research remain to fully establish the impact of the Lundy ecology on these two species and the possible trade-offs they enact. Such research should incorporate life-history variables that assess the survivorship and reproductive success of young after they leave the nest and also the survival and reproduction of adults across a number of breeding seasons, as the effects of a stressed feeding ecology could be felt at various points across the life cycle for both adults and their offspring. Future research utilising radio and GPS tracking techniques may also prove the most effective means of assessing the foraging range of these species and answering questions as to differences in where and on what HG and LBB on Lundy feed. Beyond behavioural observations, measurements of weight change across the breeding season and analyses of diet in both adults and chicks may provide complimentary data to help assess the questions addressed in this research.

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