SIBLING AGGRESSION BETWEEN BLACK-LEGGED KITTIWAKE (*RISSA TRIDACTYLA*) CHICKS

by

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ABSTRACT

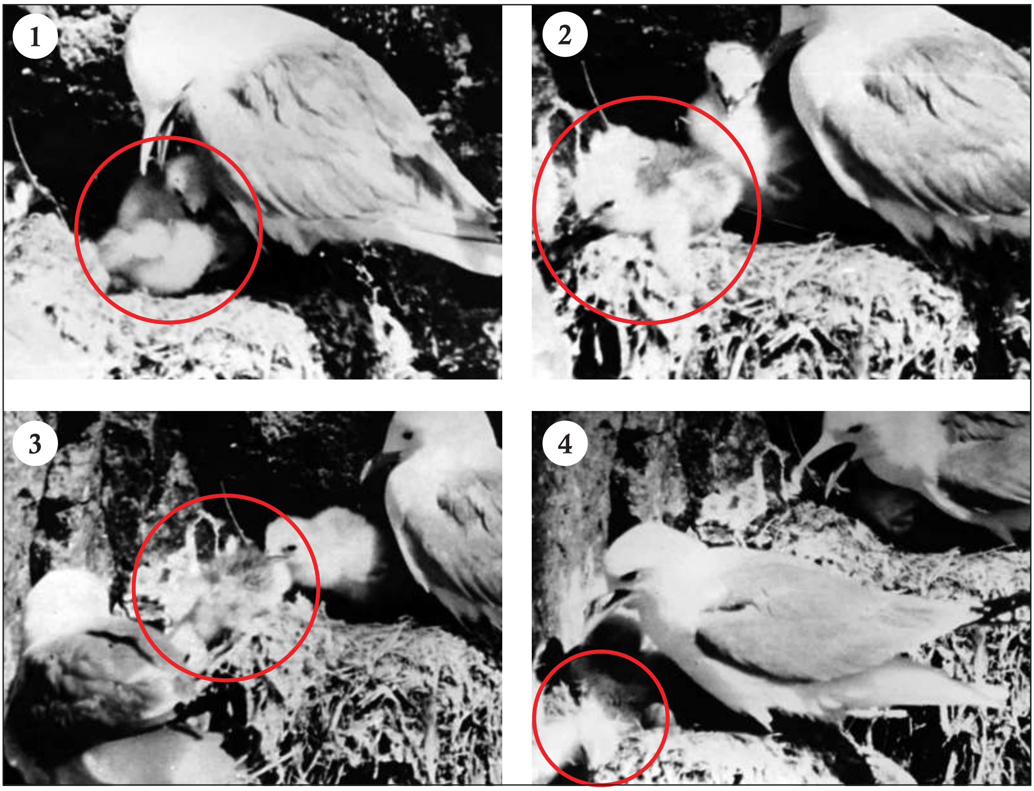
Siblicidal aggression has been documented in black-legged kittiwakes (*Rissa tridactyla*) by many researchers. First hatched (alpha) chicks attack and evict beta chicks, leading to the death of the younger bird. The infrequent nature of siblicide makes collecting consistent data difficult, but aggressive interactions between chicks are more readily captured. It is possible that patterns in aggressive behaviour will provide insight into the antecedents of siblicide. In this study, we used film footage collected during the breeding seasons from 2018-2021 to analyse aggressive interactions. First, we explored frequency differences in key behaviours between alpha and beta chicks. We then looked at the behavioural sequences within nests to describe aggressive interactions. Alpha chicks were consistently the aggressor in all samples, and beta chicks acted defensively. We comment on these findings and their relation to siblicidal aggression.

Keywords: *siblicide*, *aggression*, *sequential analyses*, *black-legged kittiwakes*

INTRODUCTION

Black-legged kittiwake, hereafter kittiwake (*Rissa tridactyla*) chicks engage in physical attacks against their siblings (Braun & Hunt, 1983; Dickins, 2021, Morandini & Ferrer, 2015; White *et al*., 2010). Attacks are characterised by pecking behaviour (White *et al*., 2010) in which one chick, almost exclusively the alpha (older) chick (Braun & Hunt, 1983; Dickins, 2021), delivers swift and often repeated directional beak jabs onto the head, body, or neck of the beta (younger) sibling. Attacks can cause the death of the beta chick (Dickins, 2021; Morandini & Ferrer, 2015). Siblicidal deaths do not usually occur on the nest (Maunder & Threlfall, 1972; Braun & Hunt, 1983) but are caused by the beta chick being forcibly evicted and falling from the nest.

Plates 1-4 show a sequence of photographs taken of a reported siblicide (D.W. Dickins, pers. comm.). In Plate 1, the alpha chick engages in a pecking attack against the beta sibling. The attacked chick faces away and tucks its beak down, an appeasement posture discussed at length by Cullen (1957) (Plate 2). As the alpha chick continues to attack, the beta chick exits the nest cup, falling into the nest below (Plate 3) where it is attacked



Plates 1-4. A sequence of images showing a siblicide event in progress. The beta chick is circled in red. The event occurred in a colony at Puffin Gully, Lundy. Images: David W. Dickins.

by the adult in that nest and forcefully ejected to its death (Plate 4). The images do not appear to show any instances of *pushes* as reported by Braun & Hunt (1983).

Siblicide is widely attributed to increased competition under food stress but has also been observed outside of feeding events. Research has primarily focused on rates of siblicide and aggression.

Studies of animal conflict increasingly use sequential analysis methods (Egge *et al.*, 2011; Trigos-Peral *et al.*, 2021) but this has not been extended to the interactions of kittiwake chicks during conflict situations. Sequential analysis enables patterns to be determined such that the likelihood of a target behaviour can be calculated from the occurrence of prior behaviours.

In the present study we used observational data collected from a population of kittiwake chicks on Lundy, to examine the behaviours of siblings immediately preceding and following pecking attacks with a view to better understanding the responses of beta chicks to attacks.

AGGRESSION

The beak is a key instrument in kittiwake encounters (Cullen, 1957). In adult kittiwakes, an attacker attempts to grasp the opponent's beak. An attacked bird may counter this by engaging in a *beak hiding* movement, tucking its beak into its body, denying the attacker access to the beak. During feeding bouts, Cullen observed that beta chicks turn their head away until the older sibling is satiated, at which point the beta chick would attempt to gain food.

According to Cullen, the beak hiding strategy is an adaptation to cliff-nesting. The behaviour serves as a method of appeasement in conflicts since there is no option to retreat given the precarious position of the nest ledge. This behavioural response suggests that beta chicks can control some aspects of aggressive encounters with their alpha siblings and avoid potential siblicide.

Research Aims

To assess differences in the frequency of key behaviours between alpha and beta chicks.
To examine conflict sequences for patterns of activity.

METHODS

We used film footage collected during the breeding seasons of 2018-2021 as a part of a long-term project studying the kittiwakes of Lundy (Dickins *et al.,* 2018). In Phase 1, we identified and selected 18 films containing two-chick nests and instances of conflict. These films were watched, and a behavioural catalogue was produced (Bateson & Martin, 2021). In Phase 2, we formally coded the behaviours on each of the 18 films.

Permissions

Ethics permission for the project was granted by Middlesex University Psychology Research Ethics Committee (Application 1114). Research and site work conformed to the Association for the Study of Animal Behaviour code of conduct and was in accordance with recommended seabird monitoring and survey methods (Walsh *et al.*, 1995). Permission was granted to collect data from the site, which is protected with restricted access. Lundy has a long history of scientific observations, established with successive wardens and is included in the Seabird Monitoring Programme (JNCC, 2021). The Warden, Dean Woodfin Jones, granted permissions for the study.

Field Site

All data were collected at the Aztec Bay inlet located on the northwest of Lundy, U.K. (51.186185, -4.674085). The site consists of steep exposed cliff faces with little vegetation which descend into the sea below. kittiwake population numbers at this colony are known to fluctuate (Jones, 2020). Kittiwakes share the site with neighbouring razorbills (*Alca torda*), guillemots (*Uria aalge*), and puffins (*Fratercula arctica*). The birds are not physically accessible to the public or researchers and suffer from no disturbance in this respect. During breeding seasons, the site experiences mild but changeable weather and can be exposed to strong winds, storms, mist, and strong sun within the range of a few hours. Average temperatures for June and July are 17°C and 19°C respectively. Plate 5 shows the site as viewed from the observation point.

Plate 5. Aztec Bay, June 2021. Image: Amanda Mead.

Data Collection

The main source of data was film footage which had been collected at the site during June and July of the breeding seasons of 2018-2021 (Dickins *et al.*, 2018). Films were created by randomly selecting nest sites to record, with a view to building an archive for future analyses. Footage had therefore not been collected directly for the present study and there was assumed to be no selection bias. All film and field data had been captured during daylight hours from 8am to 5pm. Film footage had been recorded using tripod-mounted digital video cameras with x30 and x60 digital zoom at approximately 100 metres from the nests.

Phase 1 Procedure

We developed a behavioural catalogue for chicks within the Behavioural Research Interactive Software package (BORIS version 7.10.2; Friard *et al.*, 2016; Table 1). We chose *Pecks* (Braun & Hunt, 1983; White *et al.*, 2010) and *Pushes* (Braun & Hunt, 1983) as measures of conflict behaviour. *Beak Grabs* and *Eating* were used to measure food gaining. *Facing Away* and *Beak to the Ground* were included as functions of appeasement, following Cullen (1957). *Defecation* was included as a proxy measure of satiety. A *Fall* and *Outside Nest Cup* category were each included for use in the event of an eviction or exit from the nest. Table 1 gives the behaviours with motor descriptions. We randomly sampled four films to pilot test the behavioural categories. Where behaviours occurred multiple times in succession, we coded each as a *point* event. For example, where a chick pecked repeatedly, every peck was recorded.

Table 1. Behavioural catalogue.

	Behaviour	**Description**
1	Peck	Focal animal jabs beak into sibling nestmate
2	Eating	Focal animal ingests food from adult
3	Beak Grab	Focal animal grasps adult's beak with own beak
4	Push	Focal animal moves sibling nestmate with force
5	Fall	Focal animal exits nest cup and ledge permanently
6	Facing away	Focal animal turns head and body so that the back is directed towards nestmates
7	Defecation	Focal animal visibly defecates
8	Outside nest cup	Focal animal exits nest cup onto surrounding ledge
9	Beak to the ground	Chick directs beak towards the nest floor

The film archive yielded 22 two-chick films with a mean duration of 22 minutes (median & mode=32 minutes, standard deviation=13 minutes). Films were selected if they contained physical conflict between siblings in the form of a peck or a push. Nests with no activity were omitted. As a result, 18 film samples were coded for the study.

Chicks sharing a nest were assumed to be siblings because most nest ledges sampled were positioned such that movement of chicks between nests was unlikely. Due to hatching asynchrony, alpha chicks start to grow sooner than beta chicks, and maintain a size advantage before the fledging phase. Therefore, the larger of two siblings in a nest was classified as the alpha chick. In all nests, identification of alpha and beta was clear with no ambiguity. We were able to identify individual nests from mapping conducted by the long-term research team. In this way we could assure the independence of our data points.

Phase 2 Procedure

We coded the 18 sampled films using our catalogue within the BORIS software. Observations commenced at the start of a film and used continuous observation concluding at the end of the film with every instance of a behaviour being recorded as an event.

RESULTS

Inferential statistics

We first conducted a series of Mann Whitney U tests to determine whether the distribution of core behaviours was the same across alpha (n=9) and beta (n=9) chicks. Each category was recorded as a percentage of overall behaviour emitted. As our sample size is low, we would urge caution in terms of interpreting the p-values associated with test statistics. But even when adopting a conservative $p=0.005$ to account for sample size, Table 2 clearly shows that only Pecks were unevenly distributed, and this because only the alpha chicks pecked in our sample. We can retain the null hypotheses for all other categories. The distribution of eating and defecation suggests that both chicks were equally provisioned in each nest. The distribution of facing away suggests that this behaviour is not only adopted in defence.

Table 2. Mann Whitney tests for asymmetries in the distribution of behaviour between alpha and beta chicks.

Null Hypothesis	p=
The distribution of Beak Grab is the same across categories of Chick	.258
The distribution of Pecks is the same across categories of Chick	.004
The distribution of Defecation is the same across categories of Chick	.666
The distribution of Eating is the same across categories of Chick	.489
The distribution of Facing Away is the same across categories of Chick	.113

Sequential Analysis

For each of the 18 films we generated a behavioural string using BORIS (version 7.10.2; Friard & Gamba, 2016). These strings were then used for sequential analysis in Behatrix, an additional program within the BORIS suite (Behatrix version 0.9.11; Friard & Gamba, 2021). Sequential analysis is an appropriate tool for examining interactions between a small number of focal animals (Drerup *et al.*, 2020; Cordoni *et al.*, 2022; Maglieri *et al.*, 2022). Behatrix enabled us to group all the strings together to explore the overall patterns of behavioural sequences within the 18 sampled nests (Trigos-Peral *et al.*, 2021; Drerup *et al.*, 2020). This was achieved by allocating an alpha or beta mark to each behaviour produced. In this way, for example, an *[Alpha] Beak Grab* and a *[Beta] Beak Grab* are treated as two separate begging behaviours that might occur next to one another in a string, or not. There were no *push* or *fall* events during the observations, and only one instance of leaving the nest cup. This last behaviour was therefore excluded from the analysis.

Table 3. Transition matrix for alpha and beta behaviours. The left hand column provides the first behaviour, whilst the remaining columns show the number of times that behaviour followed. For example, [Alpha] Beak Grab was followed 37 times by an [Alpha] Peck.

First Behaviour	[Alpha] Beak Grab	[Alpha] Defecation	[Alpha] Eating	[Alpha] Peck	[Beta] Beak Grab	[Beta] Beak to the ground	[Beta] Defecation	[Beta] Eating	[Beta] Facing away
[Alpha] Beak Grab	0	3	9	37	23	0	1	7	1
[Alpha] Defecation	3	0	0	0	1	0	1	0	0
[Alpha] Eating	7	0	0	3	1	0	0	5	0
[Alpha] Peck	41	0	1	0	0	4	0	3	8
[Beta] Beak Grab	17	1	0	4	0	0	2	5	1
[Beta] Beak to the ground	3	1	0	0	0	0	0	0	0
[Beta] Defecation	2	1	0	0	1	0	0	0	0
[Beta] Eating	6	0	3	8	2	0	1	0	5
[Beta] Facing away	4	1	2	6	1	0	0	5	0

Table 3 presents the transitions matrix for the entire data set representing all 18 nests. Repeated behaviours were excluded from this analysis, leaving just the one event to represent them. For example, repeated pecks would be represented as just one peck in the transition matrix. Repeated behaviours are regarded as bouts, which can indicate intensity of response, but for this analysis we were interested only in transitions between behavioural types.

Using these transitions, we then ran a permutations analysis with 102 permutations. Permutation analyses compare the actual sequence of behaviours observed with possible sequences, randomly drawn from the data set. These random draws are referred to as permutations. As we had a small data set, we ran a small number of these permutations (Knijnenburg *et al.*, 2009) to determine whether the transitions in the observed data were due to chance or not. Permutation analysis returns empirical *p-values* (alphas) for these probabilities, calculated from the actual data and not dependent upon any assumed distribution. Table 4 contains p-values after 102 permutations. Where a p-value is significant (at a conservative $p=0.005$ due to sample size) we can determine that at no point during the 102 permutations was a value equal to or higher than the number of observed transitions achieved. For example, we can see that was a significant transition at p<0.0001. If we refer to Table 3, we can see that this happened four times within the observations. Thus, no permutation returned a transition frequency .

Table 4. Permutation matrix for 100 permutations drawn from the original data. The table should be read as Table 3, but each cell contains a p value. Where p is significant then the transition is not considered random. Where p=0.000 it should be read as p<0.0001. The sample size is small, and we would recommend a conservative alpha threshold of p=0.005.

First Behaviour	[Alpha] Beak Grab	[Alpha] Defecation	[Alpha] Eating	[Alpha] Peck	[Beta] Beak Grab	[Beta] Beak to the ground	[Beta] Defecation	[Beta] Eating	[Beta] Facing away
[Alpha] Beak Grab	1.000	0.500	0.059	0.000	0.000	1.000	0.922	0.716	1.000
[Alpha] Defecation	0.363	1.000	1.000	1.000	0.559	1.000	0.137	1.000	1.000
[Alpha] Eating	0.196	1.000	1.000	0.696	0.882	1.000	1.000	0.000	1.000
[Alpha] Peck	0.000	1.000	0.980	1.000	1.000	0.000	1.000	0.951	0.049
[Beta] Beak Grab	0.010	0.500	1.000	0.931	1.000	1.000	0.186	0.196	0.912
[Beta] Beak to the ground	0.059	0.147	1.000	1.000	1.000	1.000	1.000	1.000	1.000
[Beta] Defecation	0.618	0.176	1.000	1.000	0.520	1.000	1.000	1.000	1.000
[Beta] Eating	0.843	1.000	0.157	0.137	0.863	1.000	0.422	1.000	0.000
[Beta] Facing away	0.902	0.402	0.324	0.186	0.951	1.000	1.000	0.020	1.000

From the transitions we created a schematic representation of the behavioural sequences in the form of a kinematic graph (Figure 1). The graph shows which behaviours preceded and followed one another and the transition frequencies, that is, the percentage of times a behaviour followed another (Egge *et al.*, 2011). The graph makes behavioural transition more easily understood, whilst containing all the data found in Table 3.

Alpha pecks were reliably followed by alpha beak grabs and beta beak to the ground. What is more, alpha beak grabs were reliably followed by alpha pecks and beta beak grabs, and alpha eating by beta eating (Figure 2). Combining these permutation results with the raw transition data in Table 3, it appears that Alpha chicks peck Beta chicks mostly in the context of feeding. Alphas peck the Beta, then beg whilst the Beta puts its beak to the ground in defence, and the Alpha pecks again after begging, whilst the Beta begs also. Beta chicks eat after Alpha chicks.

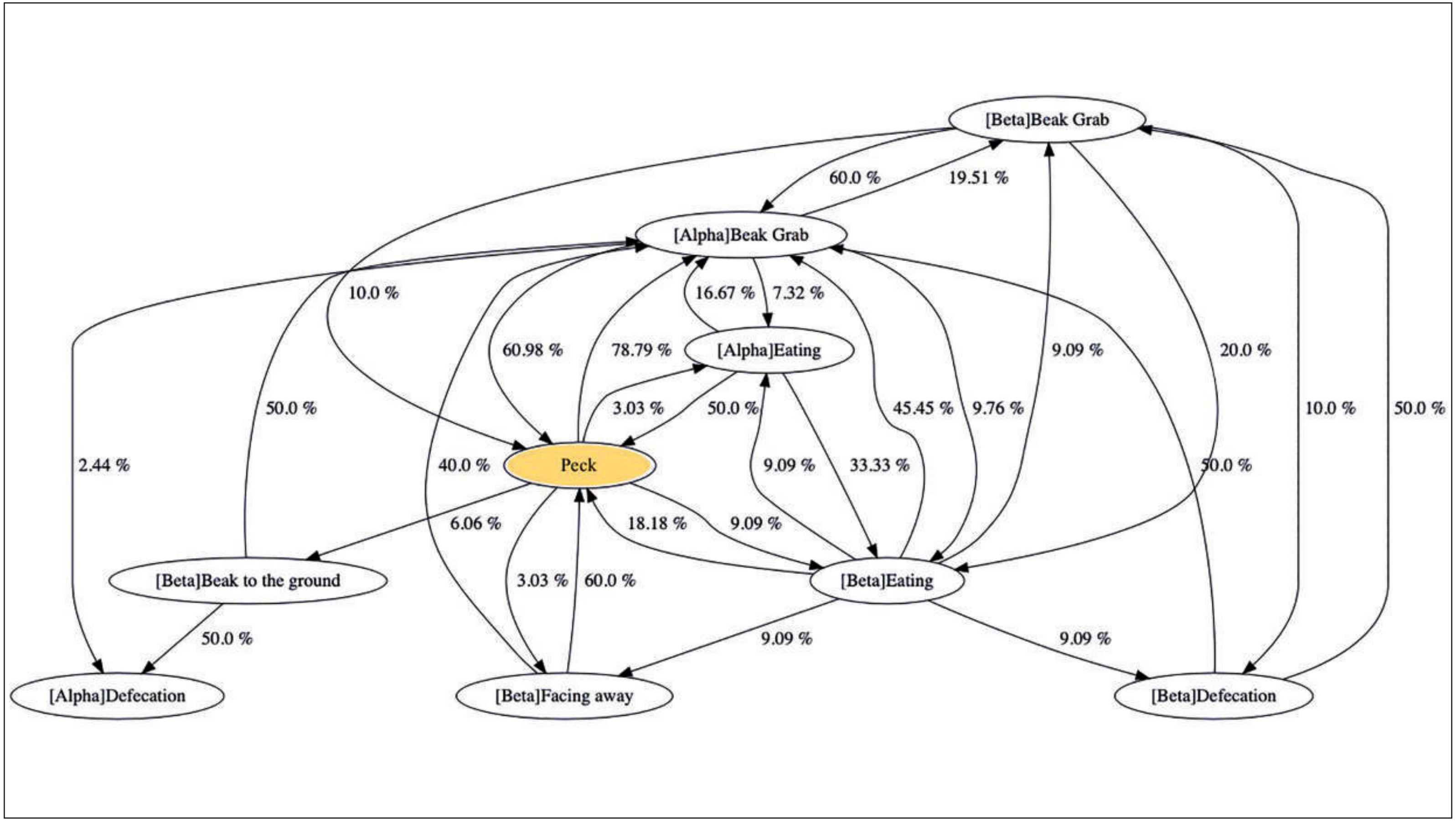


Figure 1. Kinematic diagram showing the behavioural transitions of alpha and beta chicks. Arrow direction indicates which behaviour occurs prior to a behaviour (arrow in) and which follows (arrow out). Transition frequencies are displayed as a percentage to the left of their respective arrow. See Table 3 for transition frequencies.

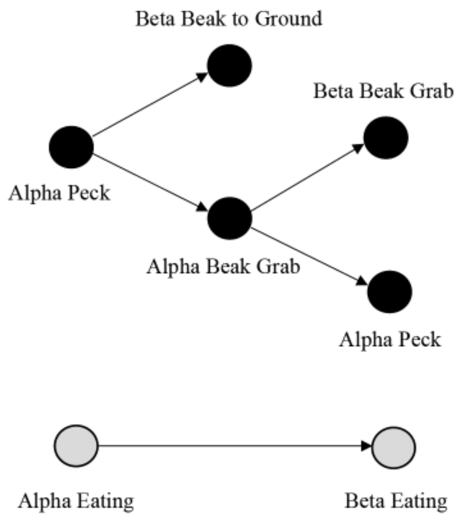


Figure 2. The main transitions in behaviour between alpha and beta chicks. As can be seen two distinct clusters of relationship emerged from the analysis.

DISCUSSION

Pecks were only delivered by alpha chicks. The behaviours of this population are therefore consistent with the literature (Cullen, 1957; Braun & Hunt, 1983). Differences in the frequencies of all other measured behaviours between the sibling groups were not significant (Table 2). As noted above, we had a small sample size, and it is possible that these null results are a consequence of this. Sequential analysis revealed that beak to the ground was performed by beta chicks in response to alpha aggression. This suggests that although chicks use the behaviour for appeasement, it is not used preventatively.

With due caution around sample size, eating was evenly distributed between alpha and beta chicks across the study suggesting that parents were provisioning their chicks equally. Kittiwakes are known to provision selectively and will allocate a greater proportion to the beta chick in the later stages of the nesting period, should the beta survive (Robertson *et al*, 2015). This study did not generate data which would allow us to test whether chicks were fed to satiation, but non-selective provisioning by parents would suggest that either there was no food stress in the colony and/or that parents were managing to find enough food. It is possible that parents of two-chick nests are of higher quality and experience than those producing one chick clutches and are therefore able to find ways to provision two chicks even where conditions are unfavourable.

To further explore these relationships a larger sample of behaviour across more nests would be desirable. It is our hope that more footage will be produced as a part of the long-term work on the island. With more data we can deploy the same analyses, but we can also begin to look to other forms of dependencies within the data. Currently we have only inspected one-step, or one-lag, transitions, asking what behaviour occurs next. It is entirely possible that a focal behaviour will in fact reliably predict behaviours further along in the sequence. To do this we would employ Markov procedures to look for dependencies, and then lag-sequential analyses to inspect them. These approaches, combined with those in this paper, would provide sophisticated association data from which to develop causal hypotheses.

Presently our transition data implies that much of the behaviour is at random, with behaviours associated with feeding providing the only clear signal. It is possible that this pattern will persist even with increased data and analyses. Kittiwakes have a small array of behaviours when chicks and producing them at random may be a part of a developmental trajectory that enables chicks to learn specific stimulus-response patterns under food reward and punishment (Dickins, 2021). From Figure 2 we can see that alpha pecking leads to beta appeasement, but also to alpha begging and then more alpha pecking. However, it also appears that beta chicks beg after alphas do. This presents the possibility that both alphas and betas will pair alpha pecking with beta begging – something that would be picked up by a lag sequential analysis. Under food stress begging should increase, in both chicks, and as a result alpha pecking may increase in intensity. What would need inspecting is whether beta appeasement reduces or has no effect upon alphas under these conditions. If this is so, then the transition to siblicide, by forcing the beta chick to shift away and fall from the nest, possibly to avoid intense pecking, becomes a quantitative matter. In other words, siblicide would not be a qualitatively different behaviour, but rather the sorry outcome of intense pecking under reduced or ineffective appeasement.

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A PRELIMINARY INVESTIGATION INTO ENVIRONMENTAL FACTORS IMPACTING THE MATERNAL BEHAVIOUR OF FERAL GOATS (*CAPRA AEGAGRUS HIRCUS*) AND SOAY SHEEP (*OVIS ARIES*) ON LUNDY

by

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INTRODUCTION

This short communication presents the preliminary findings of mother-offspring interactions in feral goats (*Capra aegagrus hircus*) and Soay sheep (*Ovis aries*) obtained between the hours of 09:00 and 17:00 during a week-long study on Lundy in late April – early May 2021. It should be noted that while this study was short in duration and limited in the time of day that observations were made, it still contributes to general understanding of the behaviour of two species of ungulates on Lundy.

METHODS

Feral goats and Soay sheep were found at Halfway Wall on the east side of the island (Figure 1). Soay sheep were found between Quarter Wall and Threequarter Wall. Subjects were nine feral goat pairs (mother and kid), and 46 Soay sheep pairs (mother and lamb).

An ethogram was used to capture behaviours observed during mother-offspring interactions (Table 1). Four researchers collected 36 10-minute continuous focal observations, which involved the behaviour of one pair being recorded continuously during each observational period.

Table 1. Ethogram of behaviours observed during mother-offspring interactions of feral goat (*Capra aegagrus hircus*) and Soay sheep (*Ovis aries*) pairs on Lundy.

BEHAVIOUR	TYPE	DESCRIPTION
Allogrooming	State	Any act of social grooming strictly between individuals in the maternal pair bond.
Suckling	State	The individual either receives or gives milk upon contact with the udder.
Calling between mother and offspring	Event	The individual calls for another individual strictly within their maternal pair bond.

At the start of each 10-minute observation, the following information was recorded:

- Percentage cover of vegetation, using a randomly placed 1 x 1 m quadrat.
- Terrain type, categorised as grassy plateau, grassy slope, rock, or cliff face.
- Wind speed, obtained from the Met Office.

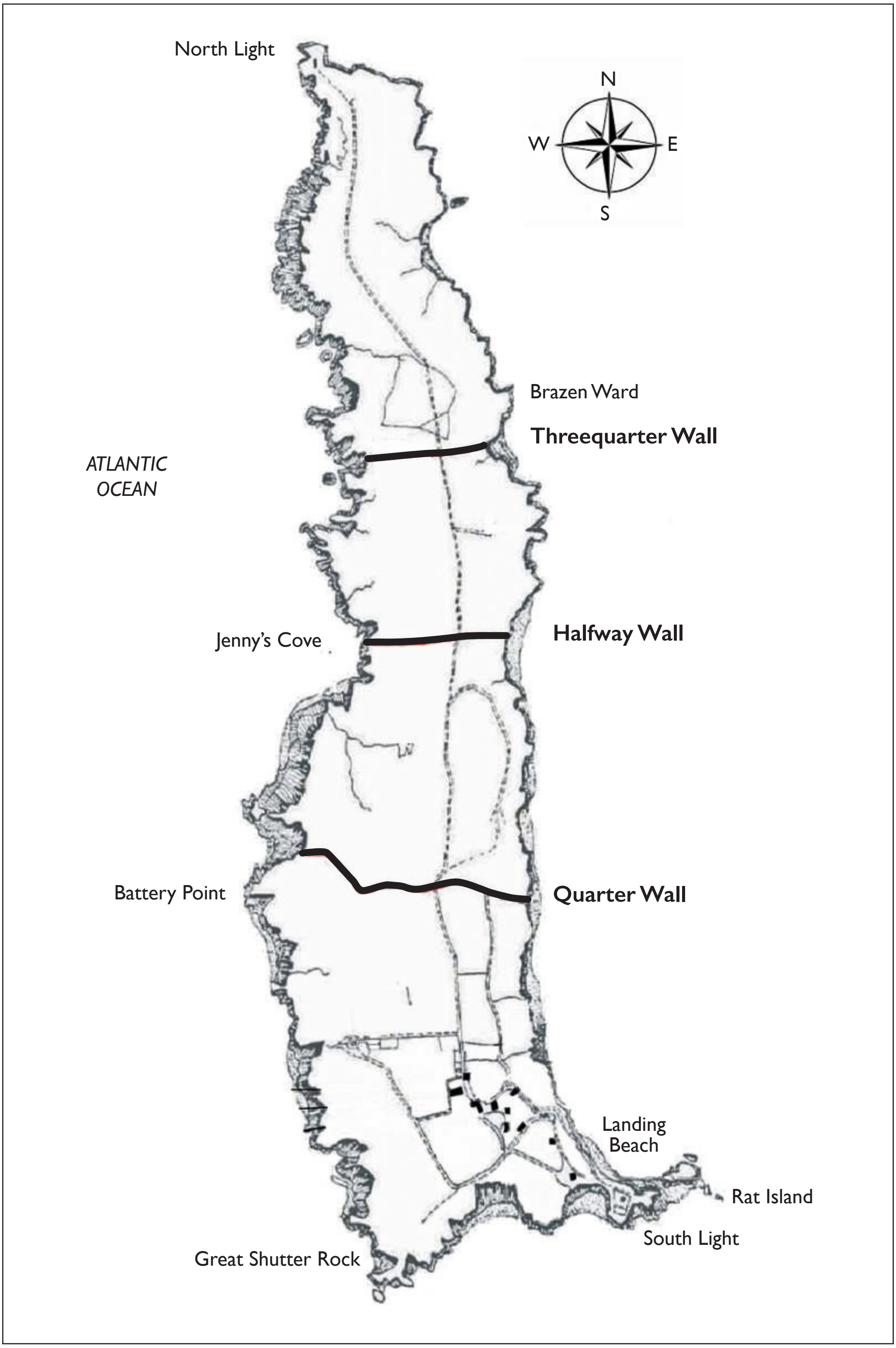

Figure 1. Map of Lundy indicating Halfway Wall, Quarter Wall, and Threequarter Wall.

- Weather type, categorised as sun, cloud, or rain.
- Time of day, categorised as morning (09:00-11:55), early afternoon (12:00-13:55) or late afternoon (14:00-17:00).

RESULTS

Three maternal behaviours were recorded (Table 2). Allogrooming and suckling were recorded in seconds, and calling was recorded in frequencies.

Table 2. Descriptive statistics including the minimum, maximum, mean, and standard deviation of the duration or frequency of observed maternal behaviours between feral goat (*Capra aegagrus hircus*) and Soay sheep (*Ovis aries*) pairs on Lundy. Behaviours were recorded within 10-minute observational periods.

BEHAVIOUR	MINIMUM	MAXIMUM	MEAN	STANDARD DEVIATION
Allogrooming	0.000	19.000	1.667	4.523
Suckling	0.000	68.000	13.639	17.437
Calling	0.000	6.000	0.4167	1.3174

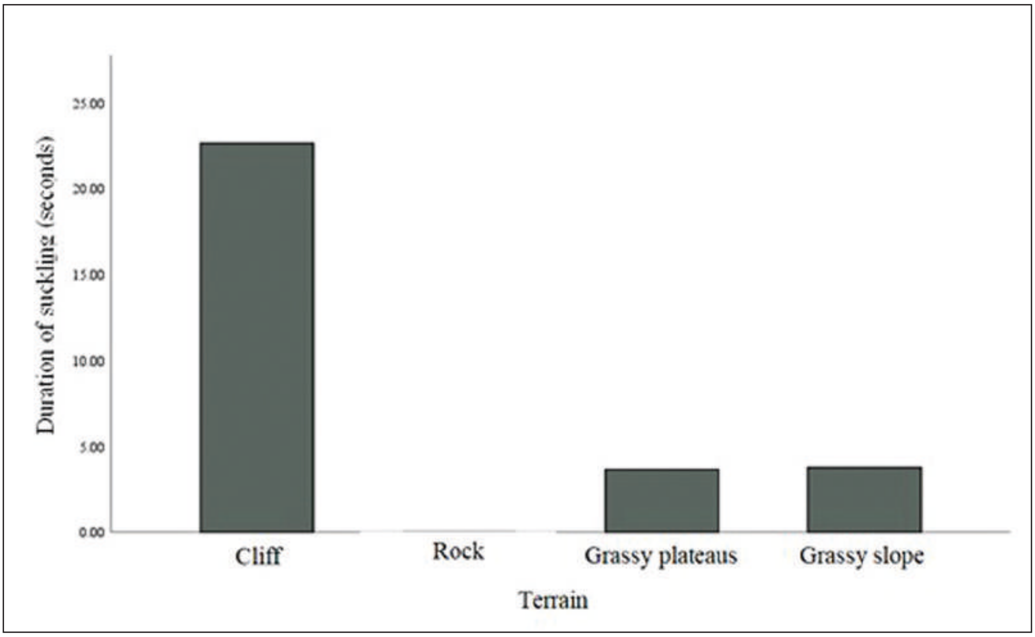

Figure 2. Relationship between terrain type and mean duration of suckling, between mother-offspring pairs of feral goats (*Capra aegagrus hircus*) and Soay sheep (*Ovis aries*) on Lundy. Suckling occurred most often on cliffs, in comparison to rock, grassy plateaus, and grassy slope terrains.

A significant relationship between terrain type and suckling was found (P < 0.001). Suckling occurred most often when the ungulates were on cliffs, in comparison to rocks (P = 0.001), grassy plateaus (P <0.001), and grassy slopes (P <0.001) (Figure 2). Allogrooming also had a significant relationship with terrain type (P = 0.001). Allogrooming occurred significantly more often when the ungulates were on grassy slopes, in comparison to cliffs (P = 0.006), rocks (P = 0.027) and grassy plateaus (P < 0.001).

CONCLUSION

The behaviours recorded in this study were allogrooming, sucking, and calling between mother and offspring. Significant relationships were found between terrain type and suckling, and terrain type and allogrooming. This study presents the preliminary findings of mother-offspring interactions in feral goats (*Capra aegagrus hircus*) and Soay sheep (*Ovis aries*), which can act as a starting point for further research.

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