Surviving Alpha: Using sequential analysis to examine the behaviours of Black-legged Kittiwake chicks during sibling pecking attacks

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Abstract

Kittiwake chicks engage in pecking attacks against their siblings, which can result in brood reduction by facultative siblicide. Attacks are almost exclusively carried out by Alpha (first-hatched) chicks against Beta (second-hatched) chicks. Onset of this behaviour is attributable to food stress brought about by environmental conditions which impact parental foraging success within breeding seasons. Size differences between siblings, due to asynchronous hatching, allow alpha chicks to dominate parental feeds and pecking attacks primarily occur during feeding events in response to beta attempts to gain food from parents. Yet attacks have been observed outside of feeding events and beta chicks can survive to fledging, even delivering retaliatory attacks in some instances. The responses of beta chicks during attacks were examined by Cullen (1957) whereby beak hiding motions by beta chicks such as facing away or tucking in the beak served as appeasement strategies and these were discussed as adaptations to Kittiwakes' habit of cliff nesting. Use of appeasement by beta chicks suggests that, notwithstanding the environmental and hierarchical factors, beta chicks have some agency in their survival through their behavioural responses to alpha siblings. In this thesis, I use sequential analysis to examine in concatenation, the behavioural sequences of alpha and beta chicks, with particular attention to those immediately preceding and following pecking attacks. In this way I hope to better understand the inter-relationship of alpha and beta chick behaviours during pecking attacks. Observations were made of Kittiwake nests using four years of archival film footage of a Lundy population. Beak grabbing was used as a specific measure of attempts to gain food from parents, as opposed to the more general begging label used in previous studies. Results found that beta chicks were only very rarely pecked when they performed the beak grab behaviour. Beta chicks were also found to use appeasement strategies in combination with food gaining behaviours. Pecking attacks did not follow where these motions were employed. Results of this study are discussed in terms of the functions of the behaviours displayed.

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I am dedicating this thesis to the ejected beta chick of 2021. You were actually very important.

Contents

Chapter 1
Introduction

Black-legged Kittiwake (*Rissa tridactyla*) chicks are known to engage in physical attacks against their siblings (Braun & Hunt, 1983; Dickins, 2021, Morandini & Ferrer, 2015; White *et al*. 2010). The intensity of these attacks can be fatal and is cited as a cause of brood reduction in the species (Dickins, 2021; Morandini & Ferrer, 2015). This conflict is characterised by harassment and dominance (Braun & Hunt, 1983) by one chick, almost exclusively the alpha (older) chick (Braun & Hunt, 1983), against a beta (younger) sibling and this frequently takes the form of pecking attacks (White *et al*. 2010). During pecking attacks, the chick delivers swift and often repeated directional beak jabs onto the head, body or neck of the sibling.

Physical attacks against siblings can be considered a form of sibling conflict or *sibling rivalry* and can be examined within an evolutionary context by discussing the possible causation, development, evolution, and function of this behaviour (Tinbergen, 1963). Questions of causation and development consider what stimuli must present to bring about a behaviour and how an organism’s life history contributed to this. Questions of evolution consider the selective pressures that brought this behaviour to exist within a population. Functional accounts seek to explain the purpose of the behaviour by considering whether it contributes to increasing the individual’s inclusive fitness.

The present study will discuss the function of physical attack interactions for both alpha and beta Kittiwake chick siblings and will use behavioural observation data to examine in detail the behaviours of chicks during these attacks.

1.1 Evolutionary considerations of sibling conflict

Inclusive Fitness Theory

According to Inclusive Fitness Theory (Hamilton, 1964), natural selection will favour traits that maximise an individual’s ability to transfer copies of its genes into future generations, indefinitely. This can occur through the reproductive success of the individual, passing on genetic copies into direct descendants (direct fitness). Further, since the goal is to maximise the continuation of genes indefinitely, the reproductive successes of those that the individual is genetically related to, for example, siblings, will also maximise the individual’s fitness (indirect fitness). Inclusive fitness is therefore the total reproductive gain of an individual through its own direct descendants plus those of its genetic relatives. Individuals should therefore be expected to behave in ways that maximise their inclusive fitness over their direct fitness.

In a line of direct descendants, the relatedness (r) between genetic relatives can be calculated starting with the individual itself who shares 100 percent of its own genes and is thus fully related to itself $(r = 1)$. It will share 50 percent of its genes with any of its direct offspring (since the other half are provided by the other parent, in a sexually reproducing species) and thus has a relatedness value to these offspring $(r = 0.5)$. This will remain the same value no matter how many offspring the individual produces. Equally, the offspring is related to its parent at this same value $(r = 0.5)$. Relatedness will then decrease with successive generations such that grandchildren will be related at $r = 0.25$, great-grandchildren $r = 0.125$ and so forth. Relatedness can also be calculated for non-direct descendants. A full sibling is related at $r = 0.5$, half siblings, nephews and nieces at $r = 0.25$, and cousins at $r = 0.125$.

Hamilton (1964) described how by using relatedness values, it was possible to calculate the conditions under which the individual will act to maximise inclusive fitness over direct fitness. The equation therefore provided a way to explain the presentation of altruism. An equation (1) of Hamilton's Rule is expressed as:

$$r(B) > c \tag{1}$$

Altruism will be favoured when the genetic relatedness (r), multiplied by the potential reproductive benefit to the recipient (B) outweighs the reproductive cost (c) to the donor. By assisting the recipient relative which bears a fraction of the donor's genes, the donor is able to increase their inclusive fitness through perpetuation of genes via the reproductive benefits to the recipient relative, which are greater than the loss of reproductive benefit to the donor.

In calculating a threshold at which an individual would favour kin over self, Hamilton's Rule also simultaneously defined an evolutionary lower limit (Mock & Parker, 1998). Where costs to the individual are not outweighed, the tipping point for altruistic behaviour is not reached, and individuals will act in favour of their own direct fitness. Parents routinely produce more offspring than they can afford to raise (Mock & Parker, 1998). In species where this occurs, and the oversupply of offspring are placed into a spatially restricted area, such as a nest, conditions for extreme competition between siblings are met (Mock & Parker, 1998). The strength of the competition may be exacerbated by environmental conditions. Where the offspring oversupply can be sufficiently provisioned, competitive behaviours may be less pronounced and this lower threshold may not even be met. Where resources do not meet a requisite supply in line with the number of offspring, selection would be expected to create mechanisms which favour the strongest in the brood.

Parent-Offspring Conflict

Overproduction of offspring may confer fitness benefits on the parent. For example, during a breeding season where environmental conditions are good with an abundance of food and all offspring can be raised successfully, this will increase the number of the parent's genetic copies going forward. In the reverse, where core members of the brood do not survive, additional offspring may serve as replacements, for example where a first-hatched chick is predated. When overproduction does not have these positive benefits, and offspring are reliant on parental provisioning, siblings will need to compete against one another.

Parents must therefore make investment decisions between siblings, but those decisions would need to maximise the parent's fitness. As such, selection should evolve proximate mechanisms that can facilitate this. According to Trivers' (1972) theory of parental investment, a parent must make decisions not only about allocation of resources to their offspring over themselves, but also about division of resources between offspring. Such trade-offs may be immediate, for example where a limited supply of foraged food must be provisioned between multiple offspring. Longer term, such as in seasonally iteroparous species, parents may need to relinquish responsibility of offspring so that they can reproduce again in their next breeding season, and as such siblings will face indirect inter-brood competition against future siblings.

Parent-Offspring Conflict Theory (Trivers, 1974) states that sibling conflict stems from parent-offspring conflicts. Considering that the relatedness values of parents to each offspring are equal $(r = 0.5)$, in a multiple offspring brood, the parent might be expected to provision each equally. However, since the offspring is completely related to itself $r = 1$, but to each sibling $r = 0.5$, each offspring will expect full investment from the parent despite the presence of siblings. Returning to Hamilton's Rule, this expectation of full investment by one sibling could be assuaged where the costs to that individual would outweigh the fitness benefits of acting for the benefit of the sibling. Where the reverse is true, competition for the full investment from the parent would ensue. A key point of Trivers' 1974 theory is that offspring are actors in their relationship with the parent, as opposed to passive vessels into which parents pour the appropriate care (Trivers, 1974). Offspring have the agency to influence parental investment in their direct fitness and, since they do not have a physical advantage over the parent, subtler forms of manipulation to maximise the allocation of parental resources are employed. This presents in the form of behaviours such as begging tactics, vocal calls and keeping in close physical proximity to the parent. While much of this communication may begin as appropriate cues which signal to the parent the offspring's genuine needs, where resources become strained, offspring may use dishonest signaling, for example continuing to beg even when satiated to gain additional food (Caro *et al.* 2016).

In engaging any competitive strategy to gain resource over a sibling, or indeed a parent, an individual as the agent will need to use strategies which ensure that gaining the resource does not come at such a cost as to outweigh the benefits of attaining it. Use of physical conflict for example brings potential for injury or death and in such case using signaling tactics such as displaying a dominant stance may incur less cost. Equally, submissiveness to physical conflict may be a fitness maximining strategy for a weaker opponent, so long as the physical conflict does not result in fatal injury.

Sibling conflict as a means of brood reduction

Brood reduction is an adaptive mechanism whereby the collective number of offspring is reduced through the death of younger offspring to ensure the survival of older, core offspring. Brood reduction usually occurs by starvation of the youngest offspring but in some species brood reduction takes the form of siblicide. Siblicide is the death of one sibling resulting from aggression or dominance by another sibling (White *et al*. 2010). Where an oversupply of offspring are produced (Mock & Parker, 1998), brood-reduction can facilitate the depletion of the number of offspring to an affordable level. Overproduction may confer fitness benefits on a parent with excess offspring acting as insurance where brood reduction occurs through for example predation or developmental loss. Excess offspring may also enable parents to maximise fitness according to variable environmental conditions. Lack (1947) proposed that parents will produce the maximum number of offspring which they can successfully provision under favourable conditions. If during a breeding season, conditions are such that food is abundant, parents are therefore able to maximise total reproductive output by raising a greater number of offspring. Where conditions in a breeding season turn out to be unfavourable, a parent may not be able to provision all offspring adequately, resulting in weak offspring or an entire failed brood which would have negative fitness consequences for the parent. Offspring overproduction therefore generates sibling competition which in turn can result in death of the youngest sibling (White *et al*. 2010).

According to Lack's hypothesis, a parent facilitates brood reduction by means of asynchronous hatching. Asynchronous hatching, chicks hatching in succession rather than at the same time, is enabled by both a laying gap and an incubation gap. The parent, rather than ovipositing all possible eggs on one day, will lay with a time interval often days apart. Incubation of these eggs then begins as soon as they are laid, the result of which being that chicks will hatch as soon as incubation is complete causing the first chick to have a size advantage over any later hatched chicks. By this mechanism, if food shortages arise such that supply is not sufficient for all offspring, the risk of all chicks failing is minimised by the loss of only the younger offspring. Applying Lack's hypothesis to sibling conflict, asynchronous hatching facilitates sibling conflict by conferring on earlier hatched chicks a size advantage, advantageous when competition for resources arises. Through brood reduction the parent therefore ensures the survival of its strongest offspring since the survival of one, or a reduced number of strong offspring, will have more long-term fitness benefits than a larger number of weaker offspring. Mechanisms enabling sibling conflict therefore have an adaptive function in that they facilitate maximisation of the inclusive fitness of the parent.

Chapter 2

2.1 The Black-legged Kittiwake *(Rissa tridactyla)*

Location and Range

The Black-legged Kittiwake (*Rissa tridactyla*) is a small-medium sized gull with a dispersal that ranges across the North Atlantic, North Pacific and Arctic regions. In the UK the Kittiwake has a wide dispersal with the most numerous populations being around the coast of Scotland and the Northeast. A map (Figure 1) shows the UK distribution (Mitchell *et al*. 2018). Smaller colonies are found on the Southeast and Southwestern coasts. As well as coastal nesting, some smaller colonies have been established in human-made areas including Tyneside and Lowestoft (Coulson, 1963). On the Atlantic and Southwest coasts, colonies are mainly concentrated in Wales, but small populations can be found in Devon and Cornwall and on Lundy.

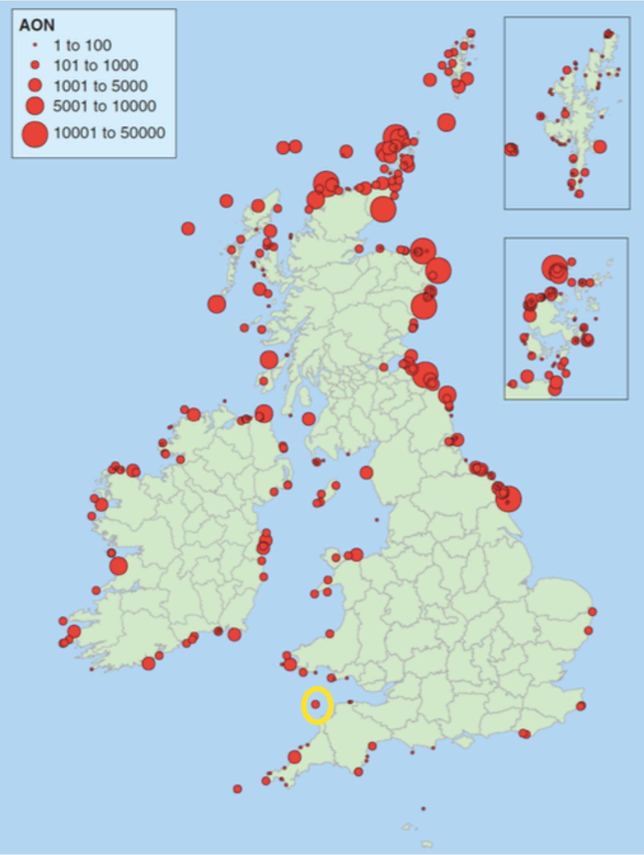


Figure 1: Map showing the distribution of Kittiwakes in the UK and Ireland 1998-2002 (Mitchell *et al*. 2018). Lundy, the site of the present study, is circled in yellow (annotation to original source).

Range

Kittiwakes spend most of the year at sea, only returning to land during the breeding season (Cullen, 1957). From March they begin to settle in colonies on shore, choosing cliff sites and more rarely but increasingly in towns and cities (Coulson, 1963). Kittiwakes have low philopatry levels and after fledging will rarely return to their natal colony to breed (Coulson, 2017) instead breeding within a neighbouring colony (Coulson & Coulson, 2008) or up to 1500km from the natal colony (Coulson & Neve de Mevergnies, 1992). In a study of two focal colonies, Coulson and Coulson (2008) found that philopatric individuals (those that have returned to breed at the colony in which they hatched) accounted for only 23% and 4.2% of the populations of the two colonies respectively. This allows for a high degree of gene flow between colonies (Coulson & Coulson, 2008), but in an isolated Kittiwake community such as Lundy, this may impact recruitment since there is no neighbouring colony and the population is therefore reliant on Kittiwakes that will travel further to reach the colony.

Coupling

Pairs may form on land or at sea within the vicinity of the breeding site (Daniels *et al*. 1994) although the nest site is usually established by unpaired males, and this is the extent of their territory (Danchin & Nelson, 1991). A pair engage in a head-tossing display (Daniels & Heath, 1984) in which either of the pair adopt a hunched position, throwing the head up rhythmically while probing at the base of the partner's beak. Females will begin to breed at 3-4 years old, while males will begin to breed at 4-5 years old (Coulson, 1966). Once partnered, most Kittiwake pairs will breed with their partner for life and divorce rarely, although 36% will take a new mate in a breeding season (Coulson, 1966). Where adult mortality is high, Kittiwakes will necessarily find a new partner (Coulson & Thomas, 1985) and this accounts for 11% of pairings (Coulson, 1966). These figures are averages across the breeding lifetime and older pairs are more likely to retain a mate (Coulson, 1966). Non-monogamous pairings, for example two females which breed with one male within the same breeding season, have been observed where there is a shortage of males within the colony (Coulson & Thomas, 1985). Kittiwakes are considered a long-lived species and can live up to 25 years, continuing to breed in the latter half of their life (Coulson & Woollner, 1976). Once a pair have established a nest site, they display high levels of long-term fidelity to nest sites, returning to those sites for successive breeding seasons.

Nest Building

Nest materials are commonly mud, grass and seaweed which is then bound together with guano. Kittiwakes will often collect their nest materials as a group alongside other Kittiwakes. It is possible that this social organisation is a strategy to provide protection from predators (Cullen, 1957). The nest is formed by trampling, shaping and sideways rhythmic manipulation of nest material (Danchin, 1991) to form a deep nest cup which is deeper than that of other gulls (Cullen, 1957). Nests are sited on narrow ledges within cliff faces. Kittiwake colonies can be crowded, and nests may be in close proximity to the nearest neighbour such that a chick from one nest could feasibly walk or fall into a neighbouring nest. Once established, Kittiwakes will continuously attend their nest to avoid pilfering of material by other birds and this attendance will continue post laying and hatching of chicks until chicks are around 15 days old (Danchin, 1987).

Reproduction

Kittiwakes produce clutches of between one and three eggs with an average clutch size of 1.0-1.7 (Coleman *et al*. 2011). Clutches of four chicks have been counted (Coulson & Thomas, 1985) but these are extremely rare and are the result of non-monogamous males copulating with more than one female but all using the same nest. T. E. Dickins *et al.* (2018) calculated average clutch size in a Lundy population at 0.93 in 2015 and 1.42 in 2016. Kittiwakes lay asynchronously and the laying gap may be between one to three days. Once the first egg has been oviposited, incubation commences and continues for around 27 days (Coulson & White, 1958) with care from both parents. If an egg fails, the female parent may lay another (Maunder & Threlfall, 1972). Second eggs are smaller than first laid eggs. Maunder and Threlfall (1972) found a mean egg volume of 45.4cc for first laid eggs in two egg clutches and 43.3cc for second laid eggs. Eggs from one egg clutches by comparison had a lower volume than both at 43.0cc. If an egg is positioned near the rim of the nest, parents will not retrieve it and it will be neglected (Danchin, 1991; Cullen, 1957).

Maunder and Threlfall (1972) found a mean laying gap between first and second eggs of 2.67 days and that eggs are laid at random times during both day and night. The length of time between first laid eggs and subsequent eggs hatching is around one to two days. This laying and hatching asynchrony facilitates a size difference between alpha and beta chicks dependent on the duration of the laying and hatching gaps.

Parental Care

Chicks are weak during their first 24 hours post-hatching but do have some ability to move about (Maunder & Threlfall, 1972). Kittiwake parents take equal responsibility for the care of offspring both during incubation and post-hatching of chicks and will alternate foraging trips with one another ensuring that one parent always remains on the nest. As chicks do not reach their optimal temperature for thermoregulation until 10 days, any chicks left unattended below this age will chill and perish. This is also the case for an unattended egg. A lack of parental attendance at the nest also leaves chicks and eggs exposed and vulnerable to predation. Given these costs, eggs or very young chicks left unattended on the nest is an indication that parents are experiencing difficulty, for example that foraging conditions are poor or that one or other parent has been lost and in such circumstances nest abandonment will ensue. Kittiwake parents only begin to recognise their offspring after around 30 days (Cullen, 1957) and as a result, chicks that exit the nest will not be retrieved by the parents.

Provisioning

Kittiwakes are pelagic seabirds catching small fish from near the surface of the water. Kittiwakes have a fairly specialist diet with a preference for year-zero sand eels (*Ammodytidae*) (Lewis *et al*. 2001) which contain rich, fatty nutrients. This specialism is in part due to the Kittiwakes' inability to dive beyond a depth of half a meter (Coulson, 2017) which limits their potential food supply. Shortages of sand eels have been linked to poor breeding success in Kittiwakes (Poloczanska *et al*. 2004), these shortages being attributed to warmer surface sea temperatures due to carbon dioxide induced climate change (Frederiksen *et al*. 2005). Kittiwakes may however move to a more generalist diet to forage other food sources and variation has been found for different geographical locations. Chivers *et al.* (2012) obtained 48 regurgitate samples from 95 Kittiwakes from two Northern Island colonies during the early chick-rearing part of the breeding season and found Clupeids to be the dominant food source.

Kittiwakes spend between 0.2-17.6 hours on foraging trips (Redfern & Bevan, 2014) and may travel up to 60km to forage (Coulson, 2017). There is evidence that in recent years, Kittiwakes are travelling further to forage in response to climatic conditions. Osborne *et al*. (2020) found that Kittiwakes foraged farther and with a more dispersed range during and following seasons of extreme marine heatwave. Increased duration foraging trips are linked to reduced breeding success as a result of greater egg predation and chick starvation due to lower rate prey delivery (Chivers *et al*. 2012). On their return adults will provision offspring by opening their beak and enabling chicks to take regurgitated food directly from inside the mouth. Unlike some other gull species, Kittiwakes do not generally regurgitate food onto the nest floor and in this respect Kittiwake chicks do not have to scrabble to be provisioned but instead must compete for their parent's attention.

Fledging

There is no one definition of fledging in the literature as chicks even after their first flight will leave and return to the nest numerous times over several days before their final departure from the natal nest. Coulson and White (1958) recorded fledging dates between 32-55 days with a mean of 42.7 days. Maunder and Threlfall (1972) assumed fledging as the time when the chick vacates the nest for more than four consecutive days and recorded a mean of 41.6 days.

2.2 Sibling conflict in Kittiwakes

In Kittiwakes, the requisite resources post-hatching are principally food, warmth, and shelter from environmental factors and predation, all of these require parental investment (Cullen, 1957). Competition for food is also competition for parental attention which is achieved by begging displays. Hatching asynchrony allows the alpha chick to monopolise the food source in this competition, both by dominating and attacking the beta chick until it becomes submissive and so makes fewer attempts to gain food, and through these attacks reduces the energy levels of the beta chick such that it is weakened.

Much of the behaviour of the Kittiwake has been attributed to their cliff-nesting habit. Cullen (1957) examined the breeding behaviour of Kittiwakes using comparative studies with ground-nesting gulls. Cullen found that attacked Kittiwake chicks display head turning behaviours in which the head is turned away or the beak tucked into the breast feathers. Cullen concluded that the conflict behaviours observed in Kittiwakes are adaptations to their cliff-nesting habit since the position of nests high on cliff ledges means they do not have the facility to retreat from attack and that the behaviours observed in beta chicks are attempts to hide the beak which serve as appeasement strategies. Cullen covered a wide scope of behaviours and included was an examination of chick behaviours in the context of sibling conflict in the Kittiwake. In ground-nesting gulls, physical sibling attacks do not appear to occur. As such, a behavioural repertoire of appeasement strategies such as are employed by Kittiwake chicks is not evident in ground-nesting chicks. Cullen tested this experimentally by artificially rearing herring gull chicks and a black-headed gull chick into a Kittiwake nest. Cullen observed that the ground nesting gulls were attacked more fiercely by the Kittiwake chicks than a Kittiwake chick would be. Cullen attributed this to the lack of a head turning strategy by the ground nesters and suggested that this behaviour must be innate. In the experiment, the edge of the nest was barriered so that escape was impossible. In ground nesting birds the strategy for escape would be to retreat and in the face of not being able to do this the chicks did not have an alternative strategy to evade attack. While the focus of the experiment was to test the presence of the head-turning response, a question here, which is not clear from Cullen’s study, is what effect the dynamics of the nestlings may have had on the intensity of the attacks delivered by the Kittiwake chicks. It is not clear from Cullen’s methodology how many chicks the artificially created nest environment contained and whether there were significant size differences between the nestlings or any of the detail of any other responses of the ground-nesters other than their lack of head-turning. There is also no reference to whether the Kittiwake chicks selected for the experiment were alpha or beta chicks. If, for example, a beta Kittiwake chick was amongst the nestmates fiercely attacking the ground-nester, then the attacking behaviour would be an example of a beta chick adopting the more dominant behaviour typically associated with alpha chicks in this instance. Equally, if the ground-nester was larger than any beta chick in the nest, it would seem unusual for a beta to attack a larger chick. Also in this situation, if two Kittiwake siblings were in the nest together with the ground-nester, what of the relationship between the siblings? Would the alpha direct attacks towards the ground-nester alone or towards both chicks? If more than one Kittiwake chick was in the nest with the ground-nester, the increased attacks against the ground-nester might be explained by a *dear-enemy* effect whereby the alpha chick withholds aggression from its Kittiwake nestmate but shows increased aggression towards the unfamiliar ground-nester (Tumulty *et al*. 2018) If attacks were directed at only the ground-nester, this would be suggestive of the alpha attempting to maximise indirect fitness and would be in line with the assumptions of relatedness under Hamilton's Rule.

While the limitations of Cullen's experiment are clear, the observation generally that Kittiwakes have a repertoire of attacking and response behaviours that ground-nesting chicks do not have, has implications for consideration of a trade-off between direct and indirect fitness for chicks. Ground nesting gull chicks suffer a great predation threat, and on this basis the fitness benefits of having a sibling in the nest for a ground nesting chick are clear. To weaken or cause the death of a sibling would increase a chick's probability of being picked off in a predation attempt, thus siblings are an insurance policy for a ground nesting chick. In contrast, Kittiwakes suffer fewer predation risks and as such a Kittiwake has less need for its sibling to assist its own survival.

The beak is a key factor in Kittiwake fighting encounters (Cullen, 1957). In adult Kittiwakes, an attacker fights by attempting to grasp the opponent's beak. Cullen proposed that the beak acts as a releasing stimulus and observed that an attacked bird will engage in a *beak hiding* movement whereby it tucks its beak into its body thus denying its attacker access to its beak. This motion in turn often results in the attacker ceasing the attack. Cullen deduced that the removal of the beak from view appeases the attacker and attempted to experimentally test the significance of the beak by presenting faux intruder Kittiwakes on nests. These intruders were in the form of fashioned Kittiwake heads both with and without beaks. Of 286 attacks on the models, 98% were directed at the beak. It appears from Cullen's discussion that the responses were too few to power firm conclusions, nevertheless the model with the beak received more attacks than the model without. Cullen also mentioned that in an attack scenario, the pacifying beak hiding behaviour occurred when the attacked bird seemed too frightened to fight back. Cullen observed that the beak hiding tactic was mirrored in chicks. Cullen uses the term *head turning* here rather than beak hiding but appears to use the terms synonymously. Chicks' head turning according to Cullen serves to appease an alpha chick. Cullen observed that a beta chick would turn their head away until its older sibling was satiated, at which point the beta chick could attempt to gain food without reprisal. Cullen observed that pecks and the adoption of a pre-peck stance by the alpha chick occurred as soon as a beta chick attempted to gain food after a parent arrived to feed the chicks. In provisional viewing of the film footage for the present study, there are instances in which attacks by alpha occur towards beta with no movement by the adult to attempt to feed beta. Also, by turning away, the beta chick removes from alpha's sight the object with which it gains food. We might predict that where a beta chick is adept at beak hiding in the early stages of life, it may increase its likelihood of surviving to fledging. On that basis, we might expect to observe beak hiding even in older chicks also.

Figures 2 and 3 show images taken from film footage of an alpha and beta Kittiwake sibling pair during a pecking sequence. The alpha can be seen to posture over the beta chick. During the film from which the images are taken, the alpha delivers a series of swift pecks onto the beta chick's head (as shown in Figure 3). The beta chick's posture is such that it is turned, facing away from the older sibling. As the pecking attack progresses, the beta chick does not quite tuck the beak into the breast feathers but tucks its beak down to point towards the ground.

Figures 2-3: Images taken from film footage showing an alpha chick pecking a beta sibling. © Kirsty Neller.

Cullen's (1957) discussion of appeasement strategies by beta chicks would suggest that, notwithstanding the environmental and hierarchical factors, beta chicks have some agency in their survival through their behavioural responses to alpha siblings. Further, consideration of the function of sibling conflict must examine the behaviours of both agents in this interaction, so the question is not only, what benefits do alpha chicks gain by attacking siblings, but also what benefits do beta chicks gain from responding in the ways that they do to these attacks.

Maynard-Smith (1982) applied Game Theory to explain how selection may favour the evolution of both aggressive and non-aggressive strategies in animal conflicts, using the model of the Hawk-Dove Game. The model assumes a situation whereby, as in nature, two individuals compete for a resource. The model assumes one agent, the hawk, to use an aggressive strategy, who will always fight for the resource. The other, non-aggressive opponent, the dove, will never fight for the resource and will retreat.

Winning the contest will allow access to the resource, but the fight may cause injury which would be a cost. The outcome will have fitness consequences for each opponent in terms of the net benefits and costs (Maynard-Smith, 1982). By applying values to the benefits and costs in a payoff matrix, the potential fitness change for each opponent can be calculated (see Table 1). Cost of injury is assumed to be twice the value of the benefit as the cost of serious injury if fighting at full power would outweigh the benefit.

Table 1: Hawk-Dove payoff matrix, where total benefit (B) is valued at +50, and total cost (C) is valued at -100.

	Hawk	Dove
Hawk	$½\,B\left(\frac{50}{2}\right) - ½\,C(\frac{100}{2}) = -25$	$B = +50$
Dove	0	$½\,B\,(\frac{50}{2}) = +25$

Where a hawk encounters a hawk, each has a 50/50 chance of winning or losing. However, the hawk will also incur a cost of injury from the fight thus the cost of injury must be subtracted from the benefit of the resource. When a hawk encounters a dove, the hawk will always win and gain the full benefit; the dove encountering the hawk will win zero times. Where a dove encounters a dove, neither fight and each has a 50/50 chance of winning or losing since the resource will either go to one or the other with no cost or will be shared.

Instinctively, one would assume that a hawk strategy would be preferable as hawks always win. However, the payoff matrix shows that gaining from this interaction is only possible when countering a dove. Where a hawk fights another hawk the cost to both decreases overall fitness. Equally, it may seem detrimental to play a dove strategy since doves never win against hawks and can never receive the maximum value that a hawk could receive when countering another dove. However, without the existence of doves within a population, hawks would only encounter hawks, aggression would be high and there would be a high degree of costs in the form of injury. On this basis, were one dove phenotype mutation to invade the population, the dove would hold an advantage due to never incurring injury and over time could take over the population. Therefore, a population of only one phenotype using their relative strategy would not be an Evolutionarily Stable Strategy (ESS) (Maynard-Smith & Price, 1973 in Maynard-Smith, 1974), that is, a strategy that could not be superseded by an alternative strategy. An ESS does not have to be a good strategy that works for all individuals in a population, it only needs to be one that can be maintained over time such as an equilibrium allowing the coexistence of two opposing phenotypes (Dawkins, 2019). Selection therefore works to maintain a balanced ratio of competing phenotypes within a population.

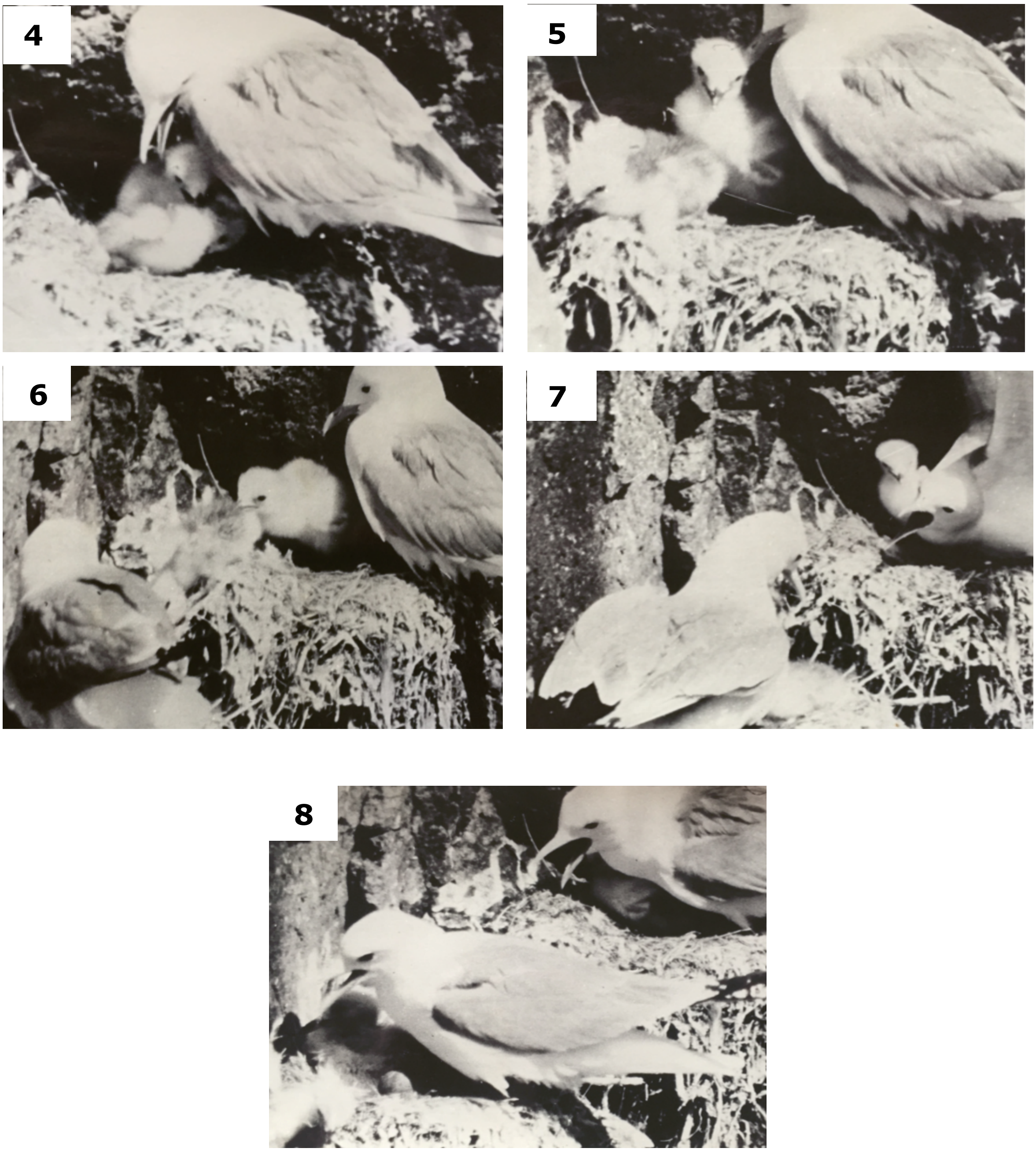
The Hawk-Dove model was designed specifically with animal contests in mind. Mapping the behaviours of alpha and beta Kittiwake chicks into the model seems fairly straightforward. Alpha (Hawk) competes with Beta (Dove) for food provisioned by the parent. We assume the relative strategies to each sibling group as we know that attacks are almost exclusively initiated by alpha chicks. The benefits to alpha of gaining the extra food would be increase to its size and strength as it grows and ultimately an overall change in direct fitness. There are also clear costs to alpha. Attacking a sibling who does not fight back does not incur any injury, however, there will be much energy expenditure in delivering the attacks. Alpha also incurs an energy cost through performing the dominant behaviour of staying continually alert to the return of the parent to intercept the food when it arrives. While alpha may receive a quantity of regurgitated fish with calorific benefit that it may not have had had it not engaged in the behaviour, it will have necessarily used up calorific energy in the pursuit of the increased movement that was required to receive that gain. Applying the values in the matrix however, we see that the model does not quite work for beta chicks. In a two-chick nest, beta only encounters alpha, and thus beta chicks would never win the resource. Since they have no other means of securing food, they would starve. We also know that unlike in the Dove scenario, beta chicks do not have an option to retreat, since they cannot leave the nest ledge. They can leave the nest cup, but this incurs costs in the form of potential chilling and lack of recognition by the parent and would be a high-risk endeavour. The overall value to beta chicks of not fighting, is not the zero value but a potential -25, the same value as hawk meeting hawk. Considering also the relative costs to alpha and beta chicks, it may even be that we should subtract a greater cost value from the beta chicks' equation. By this token, the beta chick could not be using a pure dove strategy as this would not explain the continued existence of beta chicks. Using the model, we cannot infer that the beta is also a hawk, since hawks represent aggressive individuals in a contest who fight or at least display aggressively. Two logical explanations may be inferred. Either we take the appeasement strategies of the beta chicks to be display fighting tactics in and of themselves or, we assume that the alpha chick switches between hawk and dove strategies.

Maynard-Smith (1986) suggested that individuals may also play a Bourgeois Strategy, moderating their behaviour to play hawk or dove dependent on conditions. One such condition is where ownership is established prior to the contest. If, in a contest, an individual is the owner of the resource, they would stand to incur costs by relinquishing the resource and should therefore adopt the hawk strategy to defend the resource. If they are not the owner, they should adopt the dove strategy. Since alpha chicks are first in the nest and may remain so for up to three days due to hatching asynchrony, it is logical that ownership may be assumed by alpha chicks. When the beta chick hatches and begins to attempt to gain food, nest space and parental attention, the alpha chick necessarily assumes the hawk strategy. Where a hatching gap is minimal, the assumption of ownership may be less pronounced, and the alpha chick may be expected to play dove. Kittiwake parents are known to selectively provision chicks (Robertson *et al*. 2015). Where this occurs, and the parent directs attention towards the beta chick, it may be that pecking attacks will occur with the alpha assuming ownership. Bourgeois plasticity would also allow for strategy switching depending on factors such shareability of the resource. In times when food is more abundant, there is less need for competition and the hawk strategy may not be necessary and siblings would equally act as doves. This would neatly explain the lower frequencies of pecking attacks by alpha siblings during breeding seasons with greater food availability. In this environment, alpha chicks play bourgeois. The use of strategies allows for siblings to maximise their potential fitness, and an ability to respond to competitive situations with the most appropriate strategy could be seen as a measure of fitness. Strategy switching also allows for an explanation of retaliatory pecks where a smaller hatching gap has resulted in siblings more equally matched in size. Beta chicks adopting a hawk strategy in these situations would be an indication of food stress. High rates of pecking attacks and ejection from the nest of beta siblings would suggest that the balance is unequally tipped in favour of alpha chicks under this model. However, Dawkins (2019) suggested that a strategy can be evolutionarily stable at an 80:20 ratio. It does not have to benefit everyone equally, it just has to work over time. The continued existence of beta Kittiwake chicks, in the face of dominant alphas, suggests that the coexistence is an ESS. That said, this may become less so where environmental conditions become less favourable over time. Increased food stress creating an upsurge in hawkish behaviour may lessen the overall productivity of beta chicks. Food shortage would also impact on the survival of alphas through starvation bringing about a reduction in Kittiwake numbers within a locality over time. As with Cullen's (1957) theories of appeasement strategies, Maynard-Smith's (1982) model suggests that alpha and beta chicks have agency in their competition against one another and this implies an individual's ability to adopt an appropriate strategy under varying conditions is in itself a measure of the chick's fitness.

2.3 Brood Reduction in Kittiwakes

To successfully fledge then, the young Kittiwake faces many hurdles both biological and environmental and often in combination. Climatic conditions, food availability, the quality and experience of parents, risk of predation and the potential of competition from a sibling.

Siblicide in Kittiwakes is observed as a sustained attack by one chick against its sibling resulting in the attacked chick being ejected from the nest through repeated pushing and or pecking (Braun & Hunt, 1983). It is not usually seen as a death in the nest (Braun & Hunt, 1983). Braun & Hunt (1983) neatly summarise siblicide as facilitation of ejection from the nest. Dickins (1985 in Dickins, 2021) observed siblicide in a Kittiwake nest at Puffin Gully, Lundy. Figures 4-8 show a series of photographs taken of this event (in communication with D. W. Dickins, 14/05/2021).



Figures 4-8: A sequence of images showing a siblicide event in progress. Event occurred in a colony at Puffin Gully, Lundy. © David W. Dickins.

In Figure 4, the alpha chick engages in a pecking attack against another chick which was assumed to be the beta sibling. The attacked chick displays the appeasement posture discussed by Cullen (1957), facing away and tucking the beak downwards, In Figure 5, the attacked chick is seen to be standing and moving away from the alpha and is close to the edge of the nest cup. By Figure 6 the chick has just exited the nest cup appearing to be unbalanced and falling into the nest below. The alpha chick's posture suggests that pecks or directional beak jabbing at the beta are still in progress. The chick enters a neighbouring nest (Figure 7) where it is attacked as an interloper by the adult in that nest. The adult of the neighbouring nest then ejects the beta chick (Figure 8).

Dickins (2021) discusses that observations of this kind are difficult to capture, even where there are strong indicators that siblicide may be likely within a nest and concludes that directly witnessing siblicide requires luck and patience. Data on the nuances of interactions between siblings immediately preceding siblicide are therefore largely missing from the literature, most research focusing on siblicide and aggression rates. Maunder and Threlfall (1972) in their census of 184 nests reported one confirmed instance where a chick was known to have been pecked to death on the nest, a method of siblicide not usually seen since most instances involve ejection from the nest (Braun & Hunt, 1983). Deaths of 24 chicks were recorded as 'unknown/missing' for which they suggested falling or being pushed from the nest as a likely cause. Their paper is lacking data or discussion to support this but if all the unknown/missing deaths were due to siblicide then the rate would be 46% which would bring it into line with rates recorded by Braun and Hunt in 1978 and 1979. Alternately, chicks may have died due to other causes such as unrecorded predation for example by being taken at night (Collins *et al*. 2014). Maunder and Threlfall (1972) found that siblicide was most likely to occur in the first 10 days of hatching and Braun and Hunt (1983) found that chick mortality was concentrated in the first eight days after hatching and this was mainly due to the death of the beta chick in two-chick broods. In correlation, Kittiwake chicks reach ultimate adult body temperature of 41.5 degrees at 10 days old (Maunder & Threlfall, 1972).

Since Kittiwakes hatch asynchronously, the alpha chick in a Kittiwake nest may have benefitted from being a singleton initially for a potential period of two full days. A hypothesis may be that the alpha chick takes the new beta sibling to be an interloper, that is, an alien chick that has entered the nest. On this basis, the alpha does not assume relatedness and thus does not behave altruistically towards the beta chick, but instead behaves in such a way as to maximise its own direct fitness.

Siblicide in Kittiwakes has been mainly attributed to food shortage and this relationship has been widely documented in the literature (Morandini & Ferrer, 2015). Decline in Kittiwake numbers worldwide has been attributed to several anthropogenic stressors, and principal among them is reduction in food supply. Limited availability of food impacts Kittiwakes' survival directly by reduced breeding success (Harris & Wanless, 1997) due to an insufficient supply of food to sustain the parent during incubation to fully provision chicks, or indirectly by creating conditions such that adults do not attempt breeding at all.

Egg mortality rates may be 27.1% (Maunder & Threlfall, 1972) to 31% (Coulson & White, 1958) and the average number of chicks per nest is reported to be 1.0 - 1.7 (Coleman *et al.* 2011). There is therefore a fine line whether a Kittiwake chick is a singleton in the nest or has a sibling. In Kittiwakes siblicide is facultative and the first condition to be met is therefore the presence of a sibling. An alpha chick may be the only chick and enjoy the full benefit of the parent's provisioning. Where a beta chick is present, the occurrence of siblicide is conditional upon food availability being insufficient to provision the brood (Morandini & Ferrer, 2015). As siblicide is the end result of conflict between chicks, understanding conflict can help build a picture of the stressors and circumstances that may lead to this form of brood reduction. Braun and Hunt (1983) examined factors facilitating brood reduction in Kittiwake chicks in an Alaskan population and recorded high levels of siblicide at 56% and 63% across two breeding seasons and higher aggression rates were found in nests where the beta chick eventually died.

The relationship between intra-brood conflict and food availability has been well established in both ecological and experimental settings for black-legged Kittiwakes (Irons *et al.* 1992; White *et al*. 2010). The food-amount hypothesis (FAH) (Mock *et al*. 1987) states that the amount of food available to siblings in a brood will determine probability and levels of chick aggression. White *et al.* (2010) tested the FAH experimentally in a colony of black-legged Kittiwakes on Middleton Island in the Gulf of Alaska. In a previous study, this colony had experienced very low productivity levels across 17 monitored years with an average of 0.06 chicks per nest (Gill *et al.* 2002). Productivity had been found to increase within the colony to 1.26 chicks per nest when food availability was increased by supplementation. During the White *et al.* (2010) study, artificial nest sites were built to enable clear viewing of chick behaviours during observations. Breeding pairs were divided into two groups: one supplemented with food, and one not. Parents were supplemented with food three times daily. In this way, the parents of the supplemented group had an increased ability to provision chicks. Observations of chick behaviours in each nest ran for 30 minutes. Aggression, begging and feeding frequency were recorded. Aggression was defined as pecking a sibling. An aggressive bout was any series of attacks with pauses of under 5 seconds. Intensity of the aggression was also recorded on a scale of 0 (no aggression) to 3 (intense aggression). Alpha chicks from the supplemented group received more food and displayed less aggression both in terms of frequency and intensity than alpha chicks of the non-supplemented control group. Beta chick life expectantly was highly correlated with aggression frequency and intensity and beta chick life expectancy was higher in the supplemented group at 26.20 days versus 13.59 in the control group. Life expectancy was calculated as the mean age of death or ejection from the nest. Life expectancy did not however interact with aggression intensity or frequency. Siblicide was not measured, perhaps due to the previously discussed difficulty in measuring siblicide rates, and of note is that pecks were used as the measure of aggression but that no reference was made to pushes as in the Braun and Hunt (1983) study. There is little discussion in the literature around pushes as a measure of aggression and no clear published definition for pushes, which is a limitation given that Braun and Hunt (1983) reported pushes were a cause of ejection from the nest in siblicides.

In a study of Kittiwakes on Lundy in the 1980's high rates of siblicide were recorded during the observed breeding season (Dickins *et al*. 1985, as cited in Dickins, 2021) and this coincided with the total collapse of the colony. Intra-nest aggression was observed not only during feeding bouts. Bouts of pecks were observed even when neither chick was being fed and as such did not have food as a stimulus for the behaviour. Pecking attacks by the alpha towards the beta chick during feeding and non-feeding bouts were coded as *punishing* and *siblicidal* respectively. Punishing pecks were those that occurred in response to feeding attempts by beta chicks, while siblicidal pecks occurred outside of feeding events. Pecks that ultimately lead to the death of a sibling did not occur in a feeding context (in conversation with D. W. Dickins 25/5/21). This is not to say that food is not a factor in these siblicidal pecks, and it may be that the lack of a feeding event occurring is evidence that food supply is insufficient for both chicks and a starvation point has been reached by alpha prompting the voracity of the attacks. The 2020 Lundy Warden's productivity survey reported that despite suspected siblicides, there was no indication that Kittiwakes were struggling to find food. (Woodfin Jones, 2020). Considering the food amount hypothesis, it is possible that even where parents are seen to be returning to the nest and provisioning food, those with two chicks may not be finding enough to sufficiently satiate both chicks. Compounding this is the difficulty in measuring the quantity or quality of food ingested by each chick. It is possible that both chicks have the same frequency of feeding but that when the beta chick is fed after the alpha, the quantity ingested by the beta is smaller.

Braun and Hunt (1983) recorded that not all aggressive bouts occurred after feeding events. Dickins (2021) puts forward an operant conditioning theory to explain this. An operant conditioning explanation for chick conflict would have that a feeding bout in the nest consists of a sequence of actions between the parent bird and a chick. Chicks come to recognise actions of the parent as cues for feeding and similarly that actions by a chick serve as cues to getting fed by the parent. The action in this case would be where a chick begs for food from the parent, this serves as the cue and the chick is rewarded by being fed. When the alpha chick observes its beta sibling begging for food, it anticipates a feeding bout, and attempts to dominate the beta chick to gain the food for itself. Unable to discern when the parent has no food available, when the alpha chick observes the beta chick begging, it attempts to assert dominance regardless. In a purely operant model however, there would be no basis for an alpha chick to assert dominance; there is no discernable cue to bring about the dominant or pecking behaviour. It is certainly possible that after an initial occurrence of attacking the beta sibling when it begs and then itself being fed, the alpha has received a reward and that in future interactions this experience serves as a learned behaviour through reinforcement. However, this does not explain inception of the dominant or pecking behaviour.

A test of whether beta's begging attempts have some role in cueing the alpha chick's attacks would be that we would not expect to see any conflict behaviour if there is no parent present on the nest as it is the parent that serves as the cue for conflict. This may be difficult to observe in very young chicks given the Kittiwake parents strategy of not leaving very young chicks unattended on the nest for more than a few seconds (Braun & Hunt 1983). Absence of both parent birds may be due to simultaneous foraging and indicate a shortage of sufficient food supply. On this basis we might also hypothesise that siblicide occurs outside of feeding bouts because there is no event that breaks the cycle of sequences of begging and pecking. Where an alpha Kittiwake is provisioned, the sequence is broken. This in combination with the satiation the alpha chick achieves from being provisioned adequately, eliminates the alpha chick's immediate need for food.

Reed (2015) discussed an operant conditioning framework in a study of herring gull chicks. By focusing on three nests, it was possible to record detailed behaviour during two one-hour observation sessions, one in the morning and one in the afternoon, for seven days. Distinct behaviours of both the chick and the parent birds were sampled and every instance of these was recorded during each session. Analysis showed these behaviours always occurred in a specific sequence without exception. Reed observed that a chick's approach and begging actions were responses controlled by a particular adult. This suggested that the approach and call acts as a discriminative stimulus and that the parent's bill serves as a secondary stimulus to which the chick responds by pecking at the bill and the subsequent provisioning of food reinforces the behaviour. While Reed's study examined behaviours under an operant hypothesis, it also demonstrated the use of focusing on the interrelationship of behaviours performed by individuals within a sequence of events. Examination of sequences of behaviours between individuals interacting with one another has also been used to examine play behaviours (Nolfo *et al*. 2021; Cordoni *et al*. 2022; Maglieri *et al*. 2022) and conflict interactions (Egge *et al*. 2010; Trigos-Peral *et al*. 2020). An examination of the behavioural repertoires of Kittiwake chicks in sequence with one another during conflict interactions is missing from the literature.

2.4 Current Status of the Kittiwake

UK-wide the Kittiwake has been classified as a red listed conservation priority since 2015 (Eaton *et al*. 2015) due to exponential population declines. This downward trend is mirrored worldwide. In some locations, colonies have completely disappeared or are on the verge of doing so. Apparently Occupied Nests (AON) are the recommended unit for surveying and monitoring Kittiwakes (Walsh *et al*. 1995). An AON is defined as 'a well-built nest capable of containing eggs, with at least one adult present' (Walsh *et al*. 1995). The UK population is currently recorded as 378,800 AON and represents 8% of the worldwide population. The Lundy population of Black-legged Kittiwakes (*Rissa tridactyla*) has declined exponentially since the first count in 1939 when 3,000 occupied nests were recorded, falling to 127 by 2013 (Booker *et al*. 2018). The most recent count in 2020 recorded an increase to 300 AON (Woodfin Jones, 2020).

Productivity data (a count of the number of chicks fledging) has been collected on Lundy since 2007 (Woodfin Jones, 2020). This has revealed fluctuation between years and colonies, for example falling to 0.38 in 2017 (Woodfin Jones, 2020). The most recent productivity data in 2020 showed a productivity value of 0.66 with 101 chicks fledging from the Lundy Kittiwake colonies (Woodfin Jones, 2020). Coulson (2017) attempted to calculate mean productivity required per pair of breeding birds to maintain breeding numbers and concluded that the decline in Kittiwakes was the result of mean productivity falling below 0.8. While increases in AONs on Lundy are promising, productivity data is low and does not reach Coulson's 0.8 required value. The number of Kittiwakes fledging on Lundy is therefore insufficient to replace the numbers of adults lost and maintain a stable population under Coulson's calculation. Decline in Kittiwake productivity has been found to correlate with availability of their primary food source, sand eels. In areas of Lundy there has in the past been complete collapse of colonies reported for example, the Long Roost and Puffin Gully sites (Dickins, 2021). In Puffin Gully, prior to the collapse, siblicide was reported in high numbers. In the 2020 Warden's monitoring report, predation and adverse weather were reported as sources of chick loss, as was siblicide (Woodfin Jones, 2020).

2.5 Research Questions and Hypotheses

I have used Reed's (2015) use of a schematic representation to build predictions of Kittiwake chick behaviour during conflict interactions (Appendix A, Figure 1) and to define the following aims and hypotheses for the current study:

1. Building on the work of Cullen (1957), to systematically measure the behaviours of alpha and beta chicks immediately preceding and following a pecking attack.

2. To determine whether there are differences in conflict sequences between age stages. The rationale for this being that older beta chicks have not succumbed to siblicide during the early stage of development when siblicide is most likely to occur, as in Maunder and Threlfall's 1972 study.

3. To determine whether parent presence serves as a stimulus for pecking behaviour. Pecking rates will be compared under the conditions of parent on the nest versus no parent on the nest.

4. To make formal observations of any instances of siblicide if they present and examine the transitions from the preceding events.

5. To examine the role of pushes in conflict sequences.

6. To increase knowledge of the Lundy population of Kittiwakes. Kittiwakes on Lundy have been studied for a number of years (T. E. Dickins, 2016; T. E. Dickins *et al*. 2018; Mead *et al*. 2021). Nevertheless, the Lundy population of Kittiwakes is underrepresented in the UK literature.

Hypothesis 1: A high transition frequency will be observed between begging function behaviours preceding a peck. The rationale for this being to test the hypothesis of D. W. Dickins (2021) that begging serves as a cue for pecks.

Hypothesis 2: Behaviours serving as a function for appeasement will only be observed in the non-dominant sibling during pecking attacks. The rationale for this is to formally test Cullen's (1957) theory.

Hypothesis 3: Age stage differences will be observed in the behavioural sequences.

Hypothesis 4: Pecks will only occur when a parent is present at the nest or within a few seconds of a parent returning to the nest (on the basis that the parent may be approaching the nest but is off camera).

Chapter 3
Methods

Data collection strategy

To make observations of the behavioural repertoires of alpha and beta Kittiwake chicks, a methodological approach was taken of using archival film footage and to code chick interactions within these films. A field study was also undertaken for the purpose of familiarisation with the site. Systematic observations were carried out using the film footage rather than the field study to enable accuracy in coding. Since film footage use allows for play back and slowing down the film, it was rationalised that this would yield more detail of the interaction.

Ethics permission for the project was granted by Middlesex University Psychology Research Ethics Committee, application number 1114 (Appendix A, Figure 2) and this was extended to myself as a co-collaborator on this project (Appendix A, Figure 3). In the design of the current study, ethical consideration was given to ensure sensitivity to the site and the species observed and other bird species nesting within and adjacent to the site. Passive observation was used, and all data was collected non-invasively with no nest or bird contact. Filming was undertaken from a distance of at least 100 metres from any nesting birds, either Kittiwakes or the neighbouring species. This was to ensure that no disturbance was made to nesting birds. All research and site work was carried out to conform to the code of conduct of the Association for the Study of Animal Behaviour and in accordance with recommended seabird monitoring and survey methods (Walsh *et al.* 1995). Long-term permissions have been granted to the research team to collect data on Lundy and to conduct observations at the particular site for the current study, Site FP16. This site is a designated observation site established with successive wardens and used by the Joint Nature Conservation Committee Seabird Monitoring Programme (JNCC, 2021). The Warden Dean Woodfin Jones granted permissions for this study and was kept informed of our daily presence at the site throughout the field study and during the film collection dates across 2018-2021. In addition, whilst permissions to carry out observations at this site have been granted long-term, at the commencement of each season discussions take place with the Warden to advise of any site changes and the lead researcher Tom Dickins undertakes an inspection of the site. This inspection takes the form of checking for nesting birds and for any signs of erosion to the site.

The study ran in 2 distinct phases:

Phase 1: A preparatory stage to review archival film footage held by Middlesex Behavioural Science Lab (BSL) from breeding seasons 2018-2020. Review included provisional viewing of all films to a) identify all films containing pecking attacks, and b) to build a behavioural catalogue of chick behaviours which occurred during pecking attacks and pilot this.

Phase 2: In this phase, observations were made to systematically code the 22 selected film samples from 2018-2021 using the defined behavioural catalogue. A field study took place at the site and field notes were collected to inform discussion of findings. Field observations were not included in the analysis.

The methods of this study, described below, apply to both the archival and the 2021 film footage and the field observations. The field observations differ in some respects and these differences will be highlighted under 'field observations.'

Passive observation was used with all data being collected non-invasively with no nest or bird contact.

Field Site

This study used data collected from Lundy, UK. Lundy is an island lying approximately 12 miles off the North Devon coast in the Bristol Channel. The island is characterised by a mild climate, typical of the British Isles although weather conditions are known to be unpredictable and Kittiwake breeding sites can be exposed to strong winds, storms, mist and strong sun within the range of just a few hours. Average temperatures for June and July are 17 and 19 degrees respectively. Kittiwakes are not known to breed on any stretch of the North Devon coast and there are no other islands nearby although there are some small sites in Cornwall and South Devon.

Lundy has two breeding sites which are accessible for observations at a distance of approximately 100 metres. These two distinct colonies are located at the neighbouring inlets of Aztec Bay (51.186185, -4.674085) and Aztec Zawn (51.187570, -4.674032). Both colonies are located in the northern half of the island on the west side. Both colonies have in common a fluctuation in Kittiwake numbers (Woodfin Jones, 2020). The most recent published count at the time of writing is from the 2020 Lundy Warden's report of 300 AON across the colonies (Woodfin Jones, 2020).

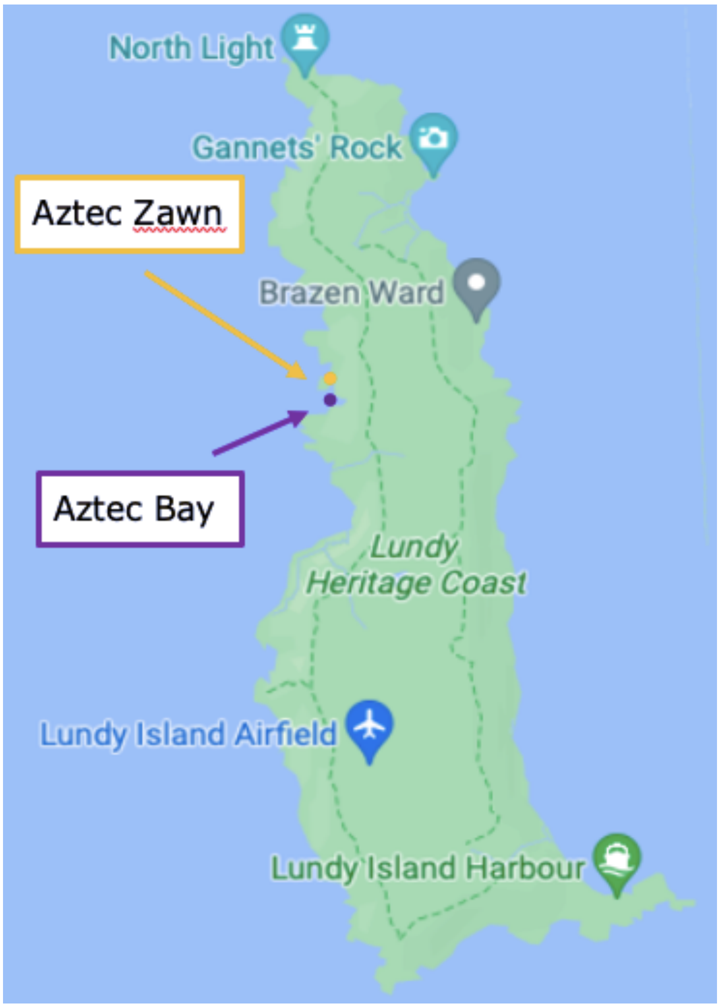


Figure 9: Map of Lundy showing locations of Aztec Bay (annotated purple) and Aztec Zawn (annotated ochre). Sourced from Google (2022).

Both sites were initially included as locations for this study. The archival footage held by our research team included nest footage recorded at both sites. Only four of the films sampled were from Aztec Zawn and as the colonies are in very near proximity (see Figure 9), and for the purpose of maximizing sample size, an assumption was applied that Kittiwakes from both colonies would be exposed to similar environmental and foraging conditions. In Phase 1, during sifting of the videos to find any instances of the target behaviour of pecks and pushes, no pecks or pushes were observed in any of the Aztec Zawn footage. Aztec Zawn films were therefore not appropriate for analysis and were eliminated from the samples for formal observation. Aztec Bay therefore became the sole site for the study.

Aztec Bay

Figure 10 shows a photo of the Aztec Bay site as viewed from the observation point during June 2021. This view is consistent with the direction of viewing used for all observations. Observers viewed the colony from an area north of the site, thus the view in the photo is looking in a southerly direction down the island.

Figure 10: Aztec Bay photo. June 2021. © Amanda Mead

The inlet that forms the site is angled such that it has a southwesterly aspect. As is usual for Kittiwakes, the colony site consists of steep exposed cliff faces with little to no vegetation and the cliffs descending directly into the sea below. Kittiwakes nest on ledges within the cliff face and these are inherently exposed to weather elements. Some nest ledges provide more shelter than others depending on factors such cliff overhang and ledge size. These factors also expose some nests to greater risk of predation. In places, nest ledges are near one another such that they provide opportunity for chicks to feasibly walk or stumble from their own nest into a neighbouring nest. Conversely, some nest sites are situated remotely with no nearby neighbour such as for example Nest 20 in Aztec Bay Panel 3 during 2021 (Appendix A, Figure 6).

The site is not exclusively inhabited by Kittiwakes. Razorbills and Guillemots nest on ledges nearby, usually within their own distinct clusters although some nests on the periphery of these may be interspersed between Kittiwake nest sites. An active puffin colony sits to the edge of the Kittiwake colony. With puffins burrowing amongst vegetation, they pose no competition for nest ledges. Using Photo 1, the puffin colony would be just beyond the right-hand edge of the photo.

The site is not physically accessible to the public or researchers due to its overhang. There is therefore no human disturbance to these nests and there was no interference from the public in the research area.

Procedure

Colony Mapping

A standardized convention for colony mapping habitually used by the Middlesex BSL research team was used to map the colony for the purpose of identifying nests. Each member of the team individually creates hand drawn maps. This is to gain familiarity with the locations of nests and to account for differences in viewing angle. Maps are then cross-checked and corroborated between the team and against photos to ensure consistency and accuracy of the nest numbers applied. A map of each panel from 2021 can be found in Appendix A, Figures 4-6. The entire Aztec Bay site is categorised into three panels. These are defined as sections of cliff face with distinct peripheries for example, a small inlet is used to divide Panel 2 from Panel 3. Three panels were defined and labelled as ABP1 (abbreviation of Aztec Bay Panel 1 and so forth), ABP2 and ABP3. Within each panel, nests were given a nest number with the nest at the highest point being Nest 1, working down through the nests, numbering them in consecutive order in approximate horizontal lines to the lowest nest. Nest numbers began from Nest 1 for each panel.

Focal Animal

Black-legged Kittiwake (*Rissa tridactyla*) chicks of between 1-55 days of age from a single colony. Precise ages of individual chicks are unknown. Upper age was estimated at 55 days in line with the upper fledging age found by Coulson and White (1958). During the 2021 field observations, chick age was often accurate due to the research team's daily monitoring from hatching. Using published guidance on estimating chick ages by sight (Thompson 2019), a nominal, categorical variable for age stage was created. All chicks were coded into one of three age stage categories:

> **Stage 1** – Downy feathers with no black markings to feathers. Chicks may shuffle around but are not fully steady on their feet. 0-8 days approximately.
>
> **Stage 2** – Black markings to feathers but with downy feathers remaining. Chicks are increasingly mobile. Wing stretches are frequent. 9-25 days approximately.
>
> **Stage 3** – Black markings and adult feathers are well formed. No downy feathers visible. Chicks may be very active. Much wing stretching and preening occurs. 26-45 days approximately.

Identifying nest occupants

Nest occupants were identified by sight as either 'alpha', 'beta', or 'adult'. Chicks were identified as either the alpha or the beta chick according to three criteria which were:

A. Size
B. Feather development
C. Locomotion

Size was the main determinant, and in most observations, chicks could be clearly categorised on size alone. A chick was in the first instance determined to be the alpha chick if it was the largest of the siblings. Where there was little obvious size difference, identification was achieved by advanced feather development in comparison to a sibling i.e., adult markings were more developed and/or there were fewer downy feathers. Locomotion or range of movements also helped to identify the alpha from the beta chick, particularly in Stage 1 chicks where alpha chicks were more steady on their feet. In all samples, the identification of alpha and beta was clear with no ambiguity.

Nest Sampling:

Only nests with two chicks were selected for sampling. An assumption was made that where more than one chick inhabited a nest, these chicks were siblings, and no interloper was present. Most nest ledges sampled were spaced apart or positioned such that movement of a chick from one nest to another appeared unlikely. Chicks were also assumed to be full siblings based on Kittiwakes' high-fidelity rates.

Nests for which observer visibility was unclear, due to being partially or fully obscured, were eliminated from the study. For example, some nests were partially obscured by overhanging cliff face. Similarly, during provisional viewing of the film footage, in some films chicks were obscured from view by an adult bird for the entire film or most of the duration of the film.

These criteria for nest sampling, focal animal and age stage identification were used for observations of both the archival film footage and the field study.

Data Collection Conditions

All film and field data were captured during daylight hours from 8am to 5pm. Weather conditions, approximate weather temperature, and wind direction data were also recorded. All filming and field observations took place approximately 100 metres from the nests. Film footage had been recorded using tripod-mounted digital video cameras with x30 and x60 digital zoom.

Archival Film Footage

A library of archival film footage recorded at the site by the Behavioural Science Lab (BSL) research team was the main source of data collection. This had been collected during June and July of the breeding seasons of 2018-2021 by Kirsty Neller and Tom Dickins. The team are experienced in collecting recordings of Kittiwake nest activity having been researching Kittiwakes on Lundy for many years. Nests selected for filming had been randomly sampled by selecting a nest number and setting that as the focal nest. The footage had not been collected for the purpose of the present study and much of the footage did not include two-chick nests. The nest footage was therefore assumed to have no selection bias.

Field Study

Field observations at the site were made between 12-19 June 2021. Field notes were collected with a view to informing discussion of findings drawn from the archive.

Chicks begin hatching in approximately the 2nd week of June so observations during these dates allowed for accurate hatching gap data between alpha and beta chicks and as a likely stage to observe nest disputes.

Phase 1 Procedure:

Film sifting for two-chick nests and presence of conflict

Phase 1 acted as a pilot study. In the first instance, it was necessary to collate all archival film files for review. Films were uploaded to an MS Teams shared drive. Selected films were downloaded to a MacBook Air 2015 (macOS 10.12 and macOS 11.4).

All film footage was provisionally viewed to identify films containing two-chick nests and any instances of pecking attacks or directional pushes against siblings by either chick. A *peck* was defined as a directional beak jab into or in the direction of the other chick. A *push* was defined as a forceful movement by one chick against another beyond general jostling or accidental bumping into. These films were labelled *conflict*. While it is acknowledged that the term conflict may have various definitions in wider usage, for the purpose of this study, conflict was used as a working term to reference physical attack. Films were observed at real time speed but slowed down where necessary and replayed where there was any ambiguity as to whether a movement had been the target behaviour or simply a generic movement.

Films containing more than one two-chick nest were watched once during sifting and all nests viewed at once for evidence of conflict. Since sifting only required assessing whether any pecks or pushes occurred, this was adequate for classifying conflict films.

Some films were continuations of other films. This was due to the method by which the archival footage had been collected as the recording equipment would only record for approximately 30 minutes at a time. This had resulted in footage of up to 90 minutes being spread across 3 consecutive files. In these cases, each of the individual films were coded as three separate observations however, if pecks or pushes had been observed in one film, the other corresponding films were also selected for sampling on the basis that conflict had been present within the full 90 minute filming of that nest.

An Excel spreadsheet was compiled listing the original footage file name (provided by Kirsty Neller), number of nests visible in the footage (some videos contained a cluster of nests) and date of first viewing of the film (to ensure none were missed). A conflict column was also included to record whether any pecks or pushes had been observed during the provisional viewing. General observations were also noted on the spreadsheet regarding such like as the general activity levels within the nest or interesting events. Of 83 available film files, 22 film samples were selected for coding, displayed in Table 2. A summary of the dispersal of number of nests, age stages and total film duration for each age stage is displayed in Table 3.

Table 2: Details of the 22 film samples selected for observation. Each sample has the original file name, duration of the film, and the year, categorised age stage of chicks in the film and plot number. Original nest number assigned by the research team is given where known.

	Film File Name	**Duration**	**Year**	**Chick Age Stage**	**Plot**	**Nest Number**
1	ABP1 8_8 JUL 2018 Btm Right 1/2	28.26	2018	Stage 1	ABP1	-
2	ABP1 1_8 JUL 2018 LEFT NEST	32.24	2018	Stage 1	ABP1	-
3	ABP1 2_8 JUL 2018 LEFT NEST	32.24	2018	Stage 1	ABP1	-
4	ABP1 3_8 JUL 2018. LEFT NEST	11.02	2018	Stage 1	ABP1	-
5	ABP1 5_8 JUL 2018	32.24	2018	Stage 1	ABP1	-
6	ABP1 7_8 JUL 2018 Btm Right 1/2	32.42	2018	Stage 1	ABP1	-
7	ABP1 9_8 JUL 2018	32.42	2018	Stage 1	ABP1	-
8	Aztec Bay (1) June 2021 ABP3	2.06	2021	Stage 1	ABP3	-
9	Aztec Bay (3) June 2021 ABP1 20	0.55	2021	Stage 1	ABP1	20
10	Aztec Bay (8) June 2021 ABP3	7.06	2021	Stage 1	ABP3	-
11	ABP1 N38 (1)-1 10_07_2021	32.38	2021	Stage 2	ABP1	38
12	ABP1 N38 (2)-1 10_07_2021	0.56	2021	Stage 2	ABP1	38
13	ABP3 Nests 14_15_13_11 (1) 22_JUL_2019	32.24	2018	Stage 3	ABP3	11
14	ABP1 Nests 17_18_22 (1) 20_JUL_2019	32.42	2019	Stage 3	ABP1	17
15	ABP1 Nests 17_18_22 (2) 20_JUL_2019	32.25	2019	Stage 3	ABP1	17
16	ABP1 Nests 17_18_22 (3) 20_JUL_2019	17.14	2019	Stage 3	ABP1	17
17	ABP3 Nests 14_15_13_11 (2) 22_JUL_2019	32.23	2019	Stage 3	ABP3	11
18	ABP3 Nests 14_15_13_11 (3) 22_JUL_2019	2.28	2019	Stage 3	ABP3	11
19	ABP2 Nest 12_11_10_7 (2) 20_JUL_2020 Right Nest	32.25	2020	Stage 3	ABP2	-
20	ABP1 N17, 18, 20 (1) 12_07_2021	32.4	2021	Stage 3	ABP1	17
21	ABP1 N17, 18, 20 (3) 12 July 2021	4.09	2021	Stage 3	ABP1	17
22	ABP1 N17,18,20 (2) 12_07_2021	32.42	2021	Stage 3	ABP1	17

Table 3: Summary the dispersal of film data across age stages.

Age Stage	No. of film samples	Total film duration hh:mm	2018	2019	2020	2021
Stage 1	10	03.50	7	0	0	3
Stage 2	2	00:55	0	0	0	2
Stage 3	10	04:16	1	5	1	3

Creating the ethogram

During sifting, chick and adult behaviours which occurred in conflict films were noted and a definition given for each. An ethogram of these behaviours was created within the Behavioural Research Interactive Software (BORIS version 7.10.2; Friard *et al*. 2016) package. Behaviours were also given a behavioural code. A random sample of four conflict films were then coded using the Observation function within BORIS. This was to test the efficacy of the ethogram. During trialing, it was evident that adults arrived and departed from nests frequently, and due to the focus of the camera zoomed in on the nests, it was not possible to see when an adult might be nearby but not on the nest. For this reason, adult presence on the nest was omitted from the study.

Ten behaviours were included in the final ethogram (see Table 4). *Point* behaviours are events which happen quickly and can be counted once. *State* behaviours are events that occur over a longer period and have a start and stop time.

Table 4: Ethogram of all selected behaviours with definitions.

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

In line with the methodology of previous studies, Pecks (Braun & Hunt, 1979; White *et al.* (2010) and Pushes (Braun & Hunt, 1979) were chosen as measures of conflict. Beak Grabs and Eating were assumed to have the functional value of gaining food and used as a measure of food gaining. Facing Away and Beak to the Ground were used as measures of appeasement in line with Cullen (1957).

Phase 2 Procedure:

Systematic behavioural coding

All selected films from 2018-2021 were coded for their full duration using behaviours from the ethogram. All nest occupants were possible focal subjects. Focal subjects were each chick and any adult bird on the nest. Footage collected during June and July 2021 was processed in the same way as the archival footage, subjected to the same conditions, using the same behavioural catalogue.

Sampling commenced at the start of a film and used continuous observation concluding at the end of the film. All observations were coded by the researcher. Films were played at full speed during inactive periods in the nest. Where events occurred, films were slowed to half speed to ensure all detail of each focal animal was coded. Every instance of any behaviour was recorded as an event. Where behaviours occurred multiple times in succession, each was coded as a point event. For example, where a chick pecked repeatedly, every peck was coded. State events (ongoing behaviours with a start and stop time) still in progress at the end of the film were given a STOP time in line with the end of the observation to avoid trailing data (T. E. Dickins, 2016).

Field Observations

After mapping the colony on the first day, a systematic sweep of the colony was undertaken at the start of each day's observations to monitor chick and egg counts for each nest. All members of the research team contributed to these counts. Through monitoring, particularly where chicks hatched during this period, approximate age of chicks was recorded in the field notes journal.

Prior to beginning field observations, a daily systematic sweep censused the colony and recorded contents of nests to monitor egg and chick numbers and any chick loss or additional chicks. Egg counts were also recorded to enable calculation of hatching gaps.

Scan sampling of the whole colony using Opticron binoculars was used to detect nest activity in two-chick nests. A telescope was then focused on any noted nest and a 30-minute observation commenced. This time was set to be broadly in line with the length of much of the films and to minimise observer fatigue. All observations included date, time of day and weather conditions. Unlike the film footage, all field observations were made in real time and thus a simplified behavioural catalogue was used. These were recorded in a field notes journal.

A design to collect repeated measures within-nest data using follow up filming on specified two-chick nests between June and July 2021 was aborted due to high levels of chick failure. On return to Lundy in July it was found that none of the chicks from the two-chick nests filmed in June had survived and therefore a follow up on those nests was not possible.

Chapter 4
Results

Analysis Strategy

Data was subjected to two distinct methods of analysis: Inferential and Sequential.

Inferential analysis used an independent measures design to compare the frequencies of behaviours between alpha and beta chicks, and the frequencies of behaviours between the three age stages. Four samples from the 22 samples were omitted from inferential testing due to containing no chick movement and therefore no data leaving 18 samples for analysis. The *nodding* behaviour was omitted from analysis. This was due to it being a state behaviour which had been measured as duration rather than frequency of occurrence. Nine behaviours were therefore analysed. A Latency category which showed mean interval between behaviours was also included as a variable. All inferential analyses were conducted using IBM SPSS version 27. As sample size was small, alpha levels were set at p=0.005 to avoid Type 1 error.

Sequential analysis examined the relative frequencies of behavioural sequences and transitions with a view to finding the most frequent pre-peck and post-peck transitions. Analysis looked at the transitions for each of the three age stages separately to examine whether pre-peck and post-peck behaviours were consistent across age stage of the chicks. Analysis was performed using Behavioural Research Interactive Software (BORIS version 7.10.2; Friard & Gamba, 2016) and Behatrix version 0.9.11 (Behatrix, Friard and Gamba, 2021). Sequential analysis is an appropriate method of analysis for examining interactions between a small number of focal animals (Drerup *et al*. 2020; Cordoni *et al*. 2022; Maglieri *et al*. 2022). Sequential analysis produces observed behaviour matrices and transitional probability matrices. The observed matrix gives the occurrence of a given behaviour following another. The transition matrix gives the transition frequency, which is the transitions converted to a percentage, i.e. the percentage of times a behaviour follows another (Egge *et al*. 2011). Behavioural strings were generated for each observation within the BORIS package (see Appendix C). Strings were grouped; all coded behavioural events for both the alpha and beta chick within an observation were combined into one string, in this way the string gives the concatenation of events as they occurred between siblings. Strings were imported into the Behatrix package and transition matrices and kinematic diagrams were generated for each age stage. These packages were chosen for their ability to perform sequential analysis of the interactions between grouped subjects (Trigos-Peral *et al*. 2021; Drerup *et al*. 2020) rather than considering each focal animal's behavioural string separately.

Inferential Analyses

Table 5 summarises the number of occurrences of behaviours for both sibling groups. Of the nine behaviors analysed, two did not occur for either sibling category during the observations. These were *fall* and *push*.

Table 5: Occurrences of behaviours for alpha and beta chicks across all samples.

Behaviour	Alpha	Beta	All occurrences
Beak grab	364	160	524
Peck	94	0	94
Eating	18	31	49
Facing away	0	19	19
Defecation	8	7	15
Beak to the ground	0	4	4
Outside of nest cup	1	0	1
Push	0	0	0
Fall	0	0	0
	485	**221**	**706**

Figures 11 to 13 show the number of occurrences of each behaviour for the two sibling groups by age stage.

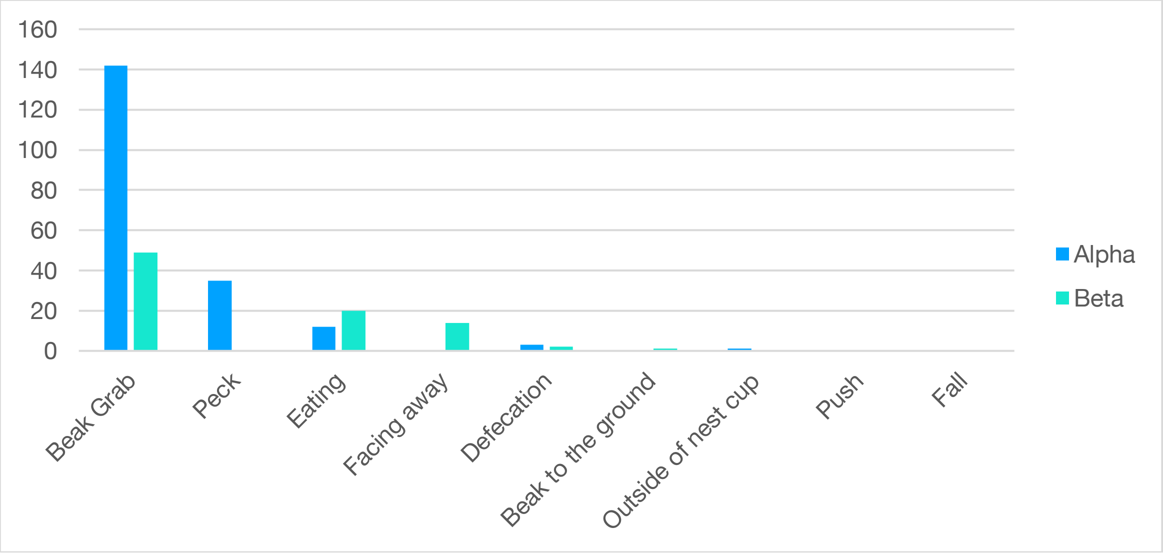


Figure 11: Stage 1 behaviour frequencies for alpha and beta chicks

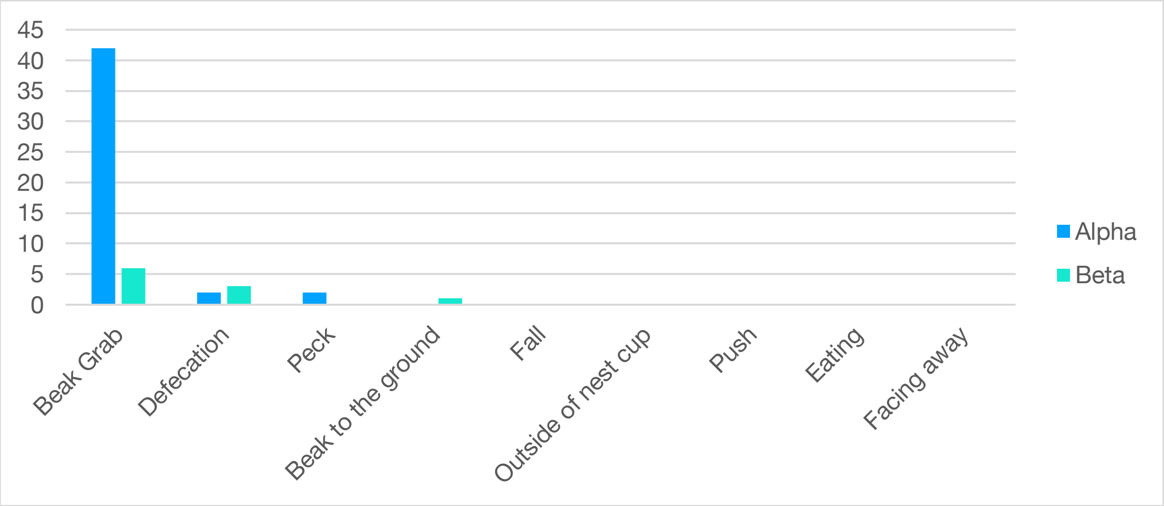


Figure 12: Stage 2 behaviour frequencies for alpha and beta chicks

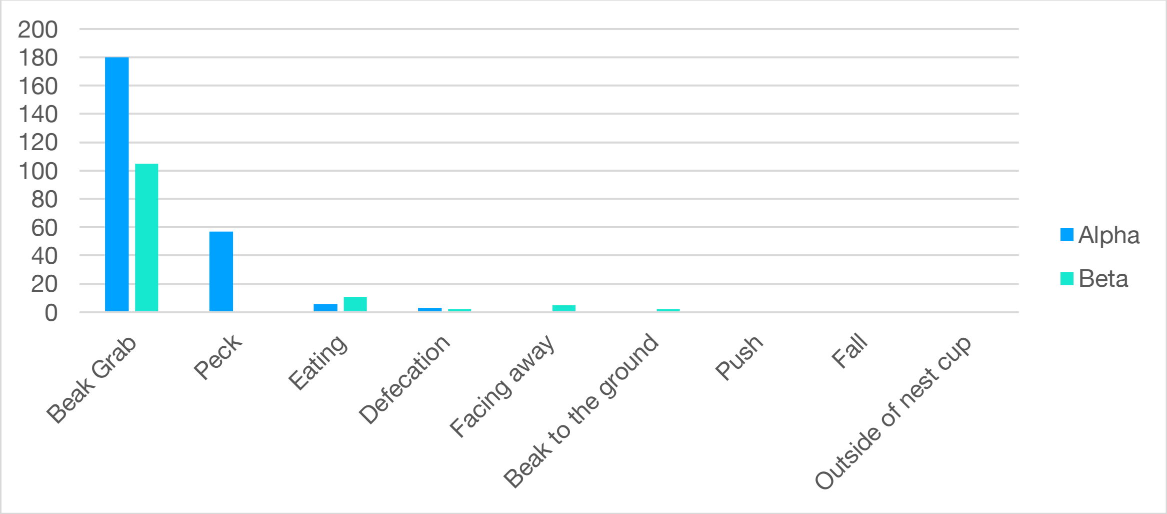


Figure 13: Stage 3 behaviour frequencies for alpha and beta chicks

Comparison of behaviours between sibling groups:

A Shapiro-Wilk test (p>0.005) together with a visual examination of histograms and Q-Q plots found that was data normally distributed for alpha beak grabs (p=0.140), beta beak grabs (p=0.477) and alpha eating (p=0.022) and beta eating (p=0.011). Data for the remaining alpha and beta behaviours were not normally distributed. See Appendix B, Table 1 for full output. Parametric testing was therefore permissible for beak grabs and eating. Levene's Test for homogeneity of variance was not significant for beak grabs (p=0.143) and eating (p=0.008). The results of two-tailed independent samples T Tests for beak grabs (t=1.784, df=16, p=0.093) and eating (t=-1.524, df=16, p=0.147) were not significant (Appendix B, Table 2).

A Kruskal-Wallis was used to test the non-parametric data. For consistency, beak grab and eating data was also included. A significant difference was found between the distributions of pecks for alpha and beta chicks (N=18, df=1, p=0.002). Figure 14 shows a box plot of these distributions. Differences in distributions for the remaining behaviours were not significant and the null for those was accepted. See Appendix B, Table 3 for full test output.

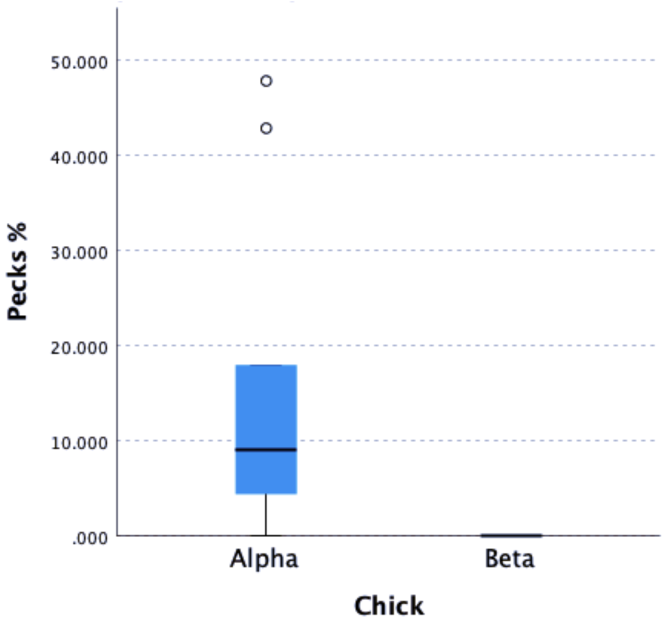


Figure 14: Box plot showing distribution of pecks for alpha and beta chicks.

Comparison of behaviours between age stages:

A Shapiro-Wilk Test found that only beak grab data was normally distributed for age Stage 1 (p=0.235) and age Stage 3 (p=0.535) (see Appendix B, Table 4 for full Shapiro-Wilk Test output). No beak grabs were recorded for age Stage 2 chicks. Since all other behaviours were non-parametric, a Kruskal-Wallis was applied to compare distributions across age stage for each behaviour. No significant difference was found between the distributions of behaviours between age stages and the null hypothesis was accepted for all (see Appendix B, Table 5 for full Kruskal-Wallis output).

In summary, the occurrences of pecking differed significantly between alpha and beta chicks. No other behaviours differed significantly in their distribution between alpha and beta chicks. No behaviours differed in distribution between age stages.

No instances of falling or pushing were recorded. Three of the behaviours were only observed in one sibling group; no pecks were produced by beta chicks and no facing away or beak to the ground events occurred for alpha chicks.

Sequential Analysis

Table 6 displays the number of sequences, behaviours, and transitions for the three age stage groups. Data was derived from 18 sequences. This represents the 18 behavioural strings generated from observations in which at least one event was recorded for both chicks (since a singular event cannot constitute a sequence).

Across all observations, the sequential analysis identified the occurrence of 13 behaviours; this was due to this analysis recording the behaviours for alpha and beta chicks as separate behaviours. Additionally, sequential analysis identified three concurrent behaviours. These were beta facing away+beak grab, beta facing away+defecation, and beta facing away+eating. Age Stage 1 chicks exhibited 13 separate types of behaviour, thus displaying the full range of behaviours recorded across the study. This was the only stage in which the concurrent behaviours were recorded. Concurrent behaviours were only performed by beta chicks.

Table 6: Number of behaviours and transitions across each age stage.

	Age Stage 1	**Age Stage 2**	**Age Stage 3**
No. of sequences	7	2	9
No. of different behaviours	13	6	9
Total behavioural events	279	56	371
No. of different transitions	42	15	33
Total transitions	272	54	362

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Pre-peck and post-peck transitions:

Initial examination of the transition frequencies revealed that across all age stages combined, and for Stage 1 and Stage 2 chicks, the most frequent pre-peck transition was a peck. This suggests a high intensity to the pecking. In Stage 3 chicks, pecks were more frequently preceded by beta facing away. Post-peck, the most frequent transition across all age stages combined was alpha beak grabs with pecks ranking second (see Table 7).

Table 7: Pre-peck and post-peck transitions frequencies across age stages with transition frequency for repeat pecks included.

	Behaviour	Stage 1	Stage 2	Stage 3	All Stages
Pre-Peck	Beta facing away	21.43 (3)	0	60 (1)	31.58 (2)
	Peck	34.29 (1)	50 (1)	41.07 (3)	38.71 (1)
	Alpha eating	0	0	50 (2)	17.65 (4)

	Beta eating	31.58 (2)	0	18.18 (4)	26.67 (3)
	Alpha beak grab	8.63 (4)	0	14.2 (5)	10.48 (5)
	Beta beak grab	4.35 (5)	16.67 (2)	0.97 (6)	2.58 (6)
Post-Peck	Alpha beak grab	42.86 (1)	0	46.43 (1)	44.09 (1)
	Peck	34.29 (2)	50 (1/)	41.07 (2)	38.71 (2)
	Beta facing away	20.00 (3)	0	1.79 (5)	8.6 (3)
	Beta beak to the ground	2.86 (4)	50 (1/)	3.57 (4)	4.3 (4)
	Alpha eating	0	0	0	1.08 (6)
	Beta eating	0	0	5.36 (3)	3.23 (5)

Transition frequencies with repeat pecks removed:

Given the high frequency of pre-peck pecks, repeat pecks were reconsidered as pecking attacks and the analysis was re-run with repeat behaviours omitted to discern which other behaviours transition into these pecking attacks. Kinematic diagrams (figures 15-17) display the transition frequencies for age stages 1-3 with repeat pecks removed. Arrow direction indicates which behaviour precedes a behaviour (arrow in) and which follows (arrow out).

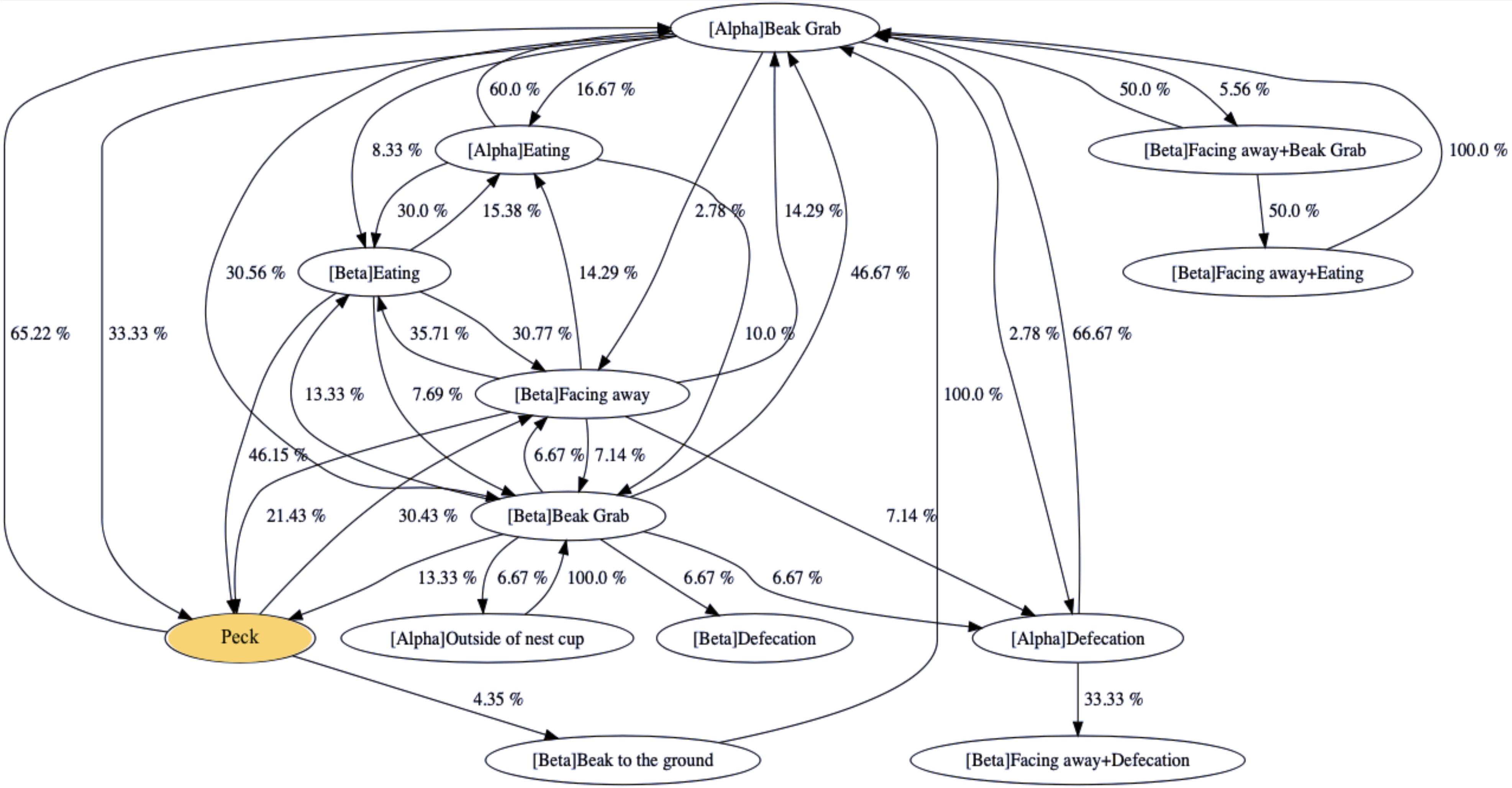

Figure 15: Stage 1 transition frequencies kinematic diagram.

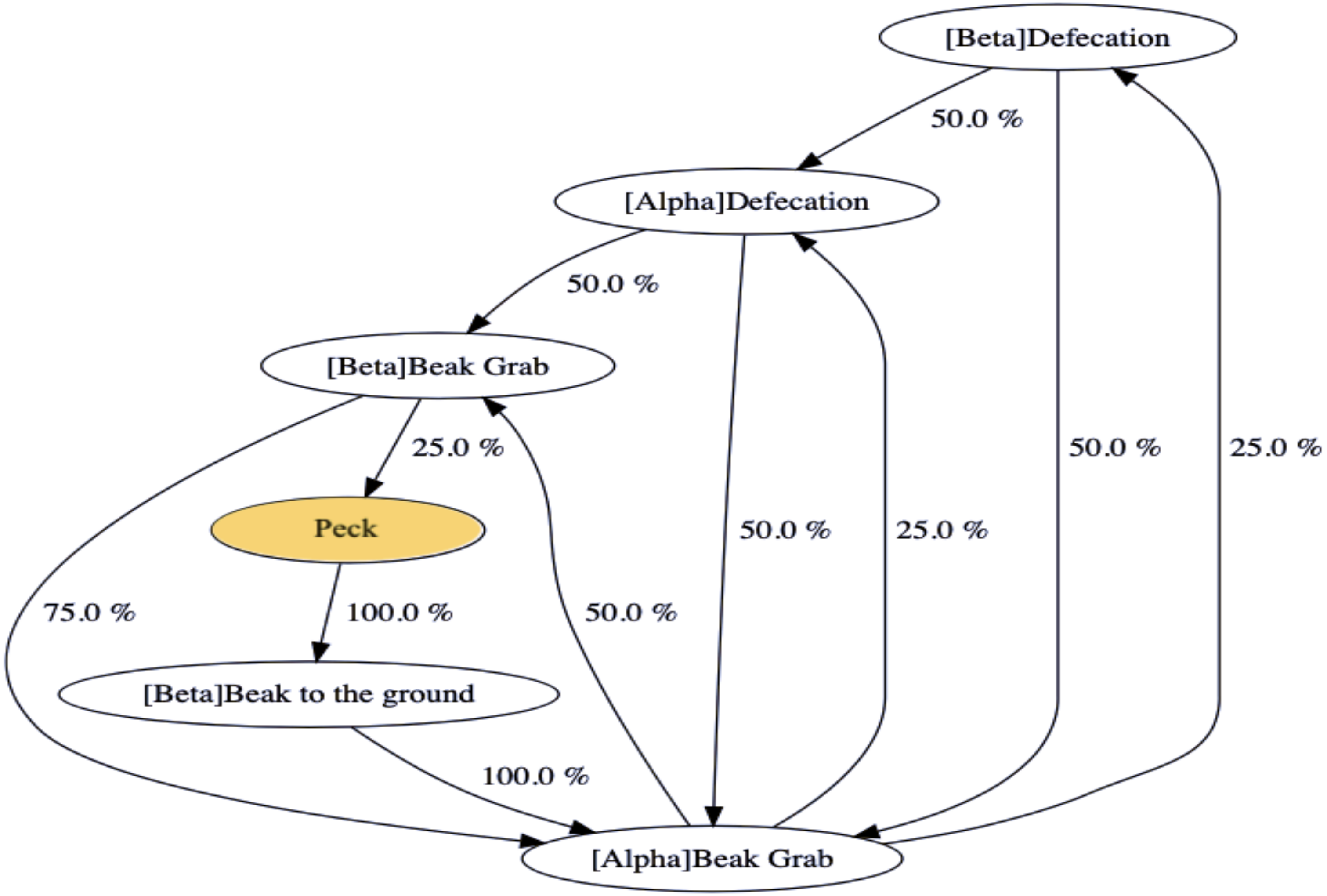

Figure 16: Stage 2 transition frequencies kinematic diagram.

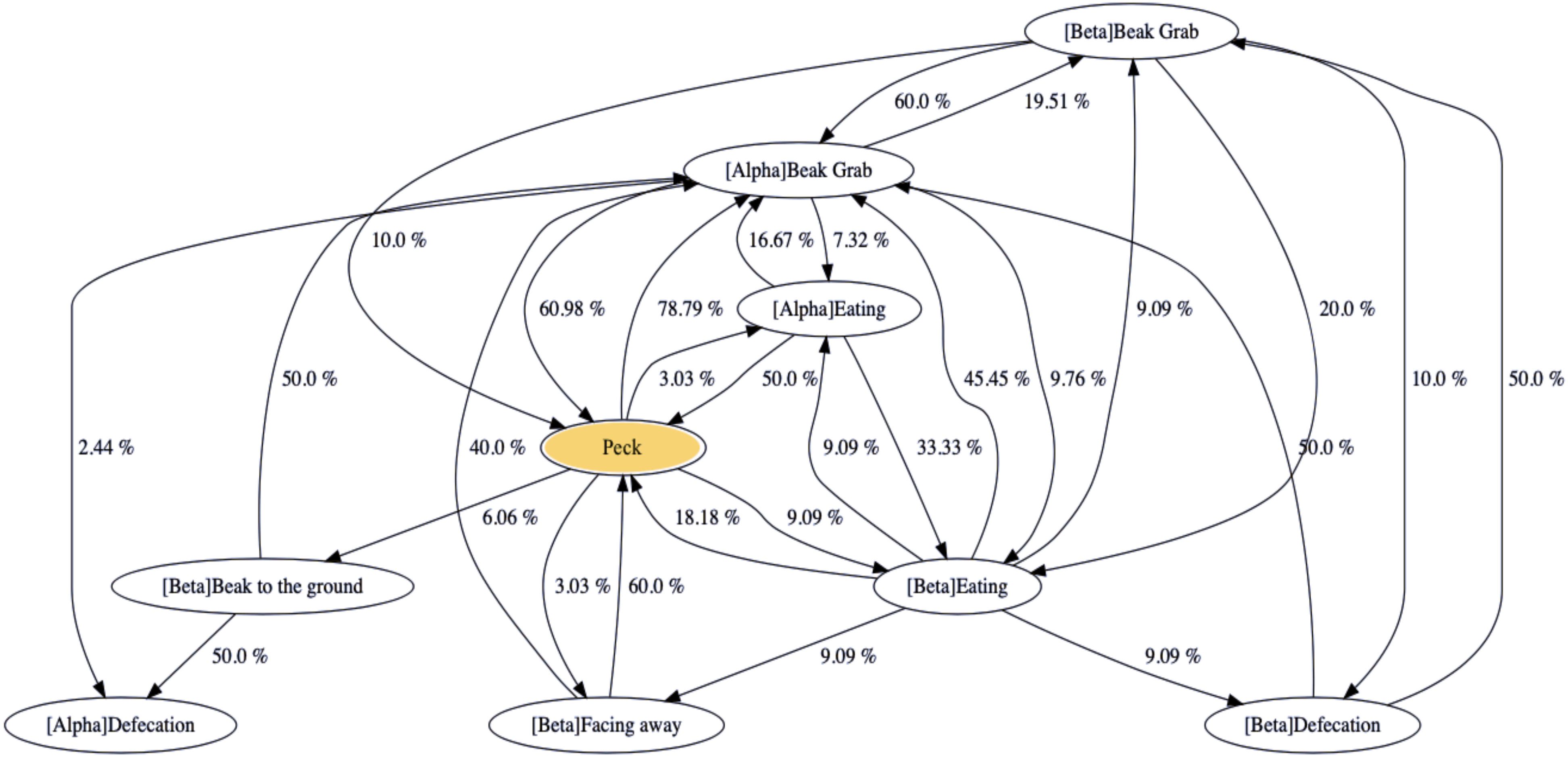

Figure 17: Stage 3 transition frequencies kinematic diagram.

Stage 1

Pre-Peck:

The most frequent pre-peck behaviour was a beta eating (46.15%). The next most frequent was alpha beak grab (33.33%) followed by beta facing away (21.43%). The lowest transition frequency was beta beak grab (13.33%).

Post-Peck:

The most frequent was an alpha beak grab (65.22%), then beta facing away (30.43%). The lowest was beta beak to the ground (4.35%).

Stage 2:

Pre-Peck:

The only observed transition preceding a peck in this age stage was beta beak grabs (25%).

Post-Peck:

The only observed transition following a peck was beta beak to the ground (100%).

Stage 3

Pre-Peck:

The most frequent pre-peck transition was the alpha beak grab (60.98%). Beta facing away was only slightly less frequent (60%). Alpha eating had a high transition (50%), followed by beta eating (18.18%). Beat Beak Grab had the lowest transition (10%).

Post Peck:

The most frequent transition was an alpha beak grab (78.79%). All other transitions were low: Beta eating (9.09%), beta beak to the ground (6.06%), and beta facing away and alpha eating having the same frequency (3.03%).

All age stages:

Pre-Peck:

The highest frequency pre-peck across all age stages was the alpha beak grab (45.68%), followed by beta eating (33.33%), beta facing away (31.58%), and alpha eating (18.75). Beta beak grabs had the lowest pre-peck frequency (13.79%).

Post-Peck:

Alpha beak grab had the highest frequency (71.93%), followed by beta facing away (14.04%), beta beak to the ground (7.02%), beta eating (5.26%), and alpha eating (1.75%).

Table 8 places these transition frequencies into rank order for pre-peck and post-peck behaviours. Behaviours highlighted in green denote those considered to have appeasement functions. A rank value of 1 = highest frequency. Rank value 0 =

behaviour did not occur immediately pre-peck/post-peck. '/' denotes rank order is tied with another behaviour.

Table 8: Pre-peck and post-peck transition frequencies across age stages converted to rank order.

	Behaviour	Stage 1	Stage 2	Stage 3	All Stages
Pre-Peck	Beta facing away	3	0	2	3
	Alpha eating	0	0	3	4
	Beta eating	1	0	4	2
	Alpha beak grab	2	0	1	1
	Beta beak grab	4	1	5	5
Post-Peck	Alpha beak grab	1	0	1	1
	Beta facing away	2	0	4/	2
	Beta beak to the ground	3	1	3	3
	Alpha eating	0	0	4/	5
	Beta eating	0	0	2	4

For pre-peck behaviour across all age stages, the removal of repeat pecks had no effect on the position of beta beak grabs in the rank order; they were still the least frequent pre-peck transition. In the Stage 2 chicks, a beta beak grab was the only pre-peck behaviour that presented. This also revealed that the most frequent transition into a pecking bout in Stage 1 chicks was beta eating but in Stage 3 this was ranked fourth. Post-peck rank order remained the same with the removal of repeat pecks (adjusted for the removal of the peck behaviour within the order system). Across all stages, a peck was rarely followed by alpha eating; in stages 1 and 2, alpha chicks did not receive food post-peck and in Stage 3 this had the joint lowest transition. The most frequent behaviour following a peck was an alpha beak grab. The two appeasement behaviours, beta facing away and beta beak to the ground, were the next most frequent post-peck behaviours. Alpha eating had the lowest post-peck transition across all ages stages and only occurred post-peck in Stage 3 chicks. Beta eating had a higher post-peck transition than alpha eating.

Zero transitions common to all age stages

Across all age stages, a peck was never preceded or followed immediately by defecation. Beta beak to the ground never preceded a peck.

The results also reveal that in no sequence was a peck ever immediately followed by a beta beak grab. Pre-peck this behaviour had the lowest transition frequency in stages 1 and 3. In Stage 2 this was the only behaviour to occur, so it necessarily had both the lowest and highest transition frequency, notwithstanding the zero ranked behaviours which did not present.

The combined facing away+ behaviours observed only in beta chicks, never immediately preceded or followed a peck. These behaviours were only produced by Stage 1 chicks.

Chapter 5
Discussion

Alpha and beta pre-peck and post-peck behaviours

Pecks were only delivered by alpha chicks, and this is in line with the literature (Cullen, 1957; Braun & Hunt, 1979). Differences in the frequencies of all other measured behaviours between the sibling groups were not significant. Sequential analysis revealed that appeasement function behaviours (facing away and beak to the ground), were only performed by beta chicks, in line with the findings of Cullen. More revealing is that the facing away behaviour was found to occur simultaneously with beta beak grabs and eating. These *facing away+* behaviours were therefore used in combination with behaviours that performed the function of gaining food. Beta chicks therefore use appeasement postures not only to pacify siblings during pecking attacks but also to gain food. Neither of these facing away+ behaviours were preceded or followed by pecks, again suggesting that these behaviours were not being used in the face of immediate attack. It is possible that pecks had occurred prior to these behaviours and lag analysis could inform this further. That the facing away was not just combined with beak grabs but also with eating confirms that this behaviour was effective for beta to be provisioned. One explanation for the use of facing away plus food gaining behaviours may be that this is part of a Kittiwakes' behavioural repertoire which can be used when faced with a dominant nestmate. In game theoretical terms this would be an effective strategy as it enables the beta chick to gain resource while minimising costs. Alternatively, it may be that this is parent-initiated behaviour. Since Kittiwake chicks have a habit of facing into the cliff (Danchin, 1991) it may be that the beta chick is simply being fed while facing away. This seems unlikely however, given that it has only been observed in beta chicks and that usually both siblings will face the parent and alternately attempt to solicit food.

Beta beak to the ground never immediately preceded pecks but did follow them in all stages. This suggests that this behaviour when used alone was used as an appeasing strategy but not preventatively. Alternatively, it may also be that this behaviour was used preventively, the result of which being that pecks did not follow. Both lag sequential analysis and/or analysis of sequences individually would be a useful future direction to determine whether this appeasement behaviour is employed in a preventative context.

A consistent pattern was that beak grabs by beta chicks, a form of food soliciting behaviour, had the lowest pre-peck transition frequency of all displayed behaviours. This was consistent across all age stages. Beta's attempts at gaining food or attention from the parent therefore were not found to directly cue alpha chicks to commence attacks on their sibling. This therefore appears to refute the hypothesis that sight of the beta chick attempting to solicit food cues the alpha to attack. However, it may be that the alpha chicks in this study had not reached starvation and that when some starvation point is reached, alpha chicks would be cued by beta's food soliciting. A further, more general point of caution in interpreting the sequential analysis is that this focuses on the behaviours immediately surrounding a peck. There is the possibility of more distal relationships between behaviours.

Behaviours across age stages

No significance was found in the differences between behaviour frequencies between the three age stages.

Pecking attacks occurred in all age stages, therefore we can conclude that while the early days of the chicks' life may be the danger period for siblicide, conflict in the form of pecking attacks continues throughout the full nestling period. It was not possible to know from the film footage whether any chicks in Stage 3 had taken first flight. As previously described, Kittiwakes may come and go from the nest once they are physically able to prior to departing the nest permanently. A point for further investigation would be whether in Stage 3 chicks, pecking attacks would be observed against beta chicks who have taken first flight. If the function of the appeasement behaviours for harassed chicks is to counter their inability to escape the attacking sibling due to the cliff-nesting situation, we might hypothesise that harassed chicks would simply fly off from the nest. This hypothesis would suggest that the beta chicks in the Stage 3 nests in this study had not taken first flight since they remained during the pecking attacks. The option to leave rather than beak hide and suffer an attack would be available, however that would also mean sacrificing access to provisioned food. A prediction here would be that as a measure of fitness, the best strategy would be to endure a pecking attack as that is less risky than not being provisioned and although the beta chick still does not engage in any reprisal attack against its older sibling, in game theoretical terms this could be interpreted as a bourgeois strategy to play dove since there is an option to behave otherwise. Plasticity to apply this strategy could also be seen as a measure of fitness. Again though, an initial course of investigation would be to determine at what age pecking attacks finally cease.

In the sequential analysis, the combined facing away+ behaviours which were performed only by beta chicks, (as discussed previously) presented only in Stage 1 chicks. That they did not occur in Stage 3 chicks may suggest that this is a faulty strategy produced only by Stage 1 chicks who do not survive beyond Stage 1. However, these behaviours never immediately preceded or followed a peck which suggests they could be a highly effective strategy which aids the beta chick in avoiding pecking attacks.

It may be that this is a strategy only needed while chicks are very young and less able to withstand pecking attacks. Further examination of these interactions, including the parent-chick interactions also would be useful to understand these behaviours further. A repeated measures design, in which facing away+ behaviours were observed in Stage 1 chicks compared against Stage 1 chicks not demonstrating this behaviour could then be compared against productivity rates for these nests. Again, there is the difficulty in how much we can ascribe chick loss in productivity data to siblicide. A greater number of samples, more targeted on 2-chick nests could reveal more of the frequency of this behaviour and whether it does present at all in Stage 3 chicks using a larger sample.

The frequency of beta facing away transitions increased between Stages 1 and 3 from 21.43% to 60%. This suggests a few possible explanations. The Stage 1 chicks in the study may have contained a mix of beta chicks, some of a phenotype which could produce this appeasement strategy under the necessary conditions, and some which would not. A hypothesis might be that not all chicks will display appeasement strategies, and these are the ones who, under strained conditions will perish. The higher frequency of pre-peck facing away observed in Stage 3 would therefore be explained by Stage 3 chicks consisting of chicks selected for due to an ability to use appeasement strategies. The remaining Stage 3 chicks may be those who had survived to that age due to conditions being more favourable in their nest, for example, experienced parents who had better foraging success, or a less dominant alpha sibling. Alternatively, facing away may have preceded pecks more often in Stage 3 as the pecks may have become more intense. As chicks increase in size with age, the demands on the parent to provision both increase also. The alpha reaches starvation point and intensifies attacks prompting beta chicks to use more exaggerated appeasement. On another note, it may be that by Stage 3, chicks have undergone some learning process, that is, that facing away is a learned behaviour.

Beta eating preceding pecks had a higher transition frequency in Stage 1 than Stage 3. This may indicate that beta chicks are simply being fed less in Stage 3 either due to reduced provisioning near to fledging or that parents struggle to provision to near fully grown chicks. However, Robertson *et al*. (2015) found that while parental provisioning of Kittiwake chicks is reduced with age of the chicks, parents increase the proportion of food allocated to the younger offspring.

In Stage 1, neither alpha nor beta chicks ever fed following a pecking attack, suggesting that parents may have had no food to provision and that attacks were being delivered due to alpha hunger rather than dominating during a feeding event. This may be indicative that had filming continued indefinitely, these pecks would have proved to be siblicidal (Dickins, 2021). In Stage 3 both sibling groups recorded eating events after pecking attacks. This may indicate that these chicks had reached this age due to successful parental provisioning either by favourable conditions or by the parents being experienced or high quality. The transition rate of pecks preceding eating was higher for beta chicks than alphas. This may be accounted for by beta chicks being provisioned a greater proportion of food (Robertson *et al*. 2015).

This may be indicative of two possibilities which would not be mutually exclusive; 1. Alpha's pecks are less intense in Stage 3 chicks, and 2. Stage 1 alpha chicks have established dominance and Stage 3 beta chicks have learnt to adopt this appeasing behaviour in situations where they anticipate a peck. An additional, and again not mutually exclusive hypothesis would be that as Stage 3 chicks are those which have survived through Stages 1 and 2, Stage 3 beta chicks have survived because of their responses to alpha attacks. A test of this would be whether, with more detailed examination of the behavioural responses of Stage 1 beta chicks, beta chicks that fledged in Stage 3 differed in their responses or response times as compared to chicks that did not survive. Again, the difficulties in tracking siblicide would need to be resolved to perform such a test.

Effect of parent presence on pecking attacks

Parent attendance on the nest was included in the behavioural catalogue and coded during observations. However, the method of coding attendance proved insufficient to identify parental presence. Adult birds came and went from the nest frequently during observations and as such parent presence on the nest as a binary present or absent measure often changed many times during an observation. This was particularly true for the Stage 3 chicks once chicks were at an age where they were not always attended. Further investigation overcoming the issue of adult arrival and departure would be necessary to determine this.

Formal observations of siblicide

No instances of siblicide were recorded in any of the observations across the four years of archival film footage or during field observations. Despite this, chick failure certainly occurred. Without direct observation, even final chick counts cannot definitively point to whether chick loss from nests was the result of siblicide. An ejection from the nest was observed during the field visit in June 2021 but this was by a probable filicide (Mead *et al*. 2021) and was not recorded for systematic analysis (see Appendix D).

A discussion of pushes

Results of the present study found no instances of pushes either in the four years of archival footage or during field observations. As siblicide did not occur during the observations of the present study, this potentially explains the absence of pushes. Much general jostling occurred during the observations but nothing that met the definition of pushes as per the ethogram. It is possible also therefore that there is some subjectivity in what researchers refer to as pushes and that pushed from the nest is used in somewhat idiomatically as a synonym for *made to leave*. Further comment on this on my part would be unwise without sight of the behaviour.

Limitations

The results of the inferential analysis which found no significance in the distributions of all but the pecking behaviour were likely affected by the small sample. Of 83 film files from the archive, only 22 were suitable for this study. Duration of the selected film samples totaled 8.21 hours and by way of comparison, Braun and Hunt (1978) captured 154.4 hours. Targeted sampling specifically of two-chick nests with good visibility would be necessary for future observation.

Small sample size also limited the sample of Stage 2 chicks. This is because the research team usually make two visits to the island during the breeding season, one when chicks are just hatching, and one when they are nearing the end of their nesting period. In 2020, due to Government restrictions, only one visit occurred, and this was mid-way through the nesting period, resulting in film footage of mainly Stage 2 chicks. Future visits to collect footage during this period would provide more data on Stage 2 chicks, however, from the results of the study, an alternative would be to omit Stage 2 as this would make for a clearer comparison between the very young chicks of Stage 1, when siblicide is most likely to present, and Stage 3 chicks.

Planned repeat observations of nests within the same breeding season were not possible due to severe chick loss by the time of the second trip to the site in July 2021. This meant that the repeated measures design of collecting data from the same chicks to compare their behaviours between Stage 1 and Stage 3 was abandoned. However, given the issues previously mentioned regarding small sample size, to implement this kind of comparison would again require observations of a much larger sample to power inferential analysis of the data. In June 2021, our initial visit to the colony presented a promising picture. There were several 2-chick nests and nests with two eggs. Chicks appeared to be feeding well and even where chicks were feeding at the same time, conflict was not observed. By July that picture had altered drastically. The colony had suffered significant chick loss and eventually, only one two-chick nest remained. Heavy rains and storms had occurred during July and this likely impacted on the colony. Bad weather may have hindered foraging attempts and lead to reduced provisioning of chicks. Failed or difficult foraging trips may also have resulted in longer absences of the parents from the nest and increased risk of predation of chicks. Younger chicks may also have suffered chilling due to low temperatures. This highlights the difficulty in using a repeated measures design. The colony on Lundy is small and it may be that to implement a repeated measures design, data collection would require sampling in a location with a much larger population.

The adult Kittiwake behavioural categories were weakly defined and not fit for the purpose of measuring adult presence or arrival on the nest. Initially, the design was to include a variable of adult present or absent on the nest for each observation. However, in most cases, parents were not consistently either on or off the nest. Thus, adult presence could not be used as a variable in this way. Separating the observation durations according to when adults were present or absent would not have been feasible for several reasons. Adults come and go with some frequency and cutting the films at these points would have led to very short observations with trailing events. Also, there will always be a point in time at which the adult, while not on the nest, is nearby or approaching and so is not truly on the nest but its presence may be affecting the chicks' behaviours. An interesting point here however would be whether the parent's nearby presence would affect chicks, since adults do not recognise their own chicks at a young age, is there any reason to suspect young would recognise a nearby adult? In the pilot stage of the study, an 'adult departs/adult arrives' type behavioural category was trialed but again this did not represent adult presence or absence as arrival of one parent often was part of a changeover between the two parents. Attempting to log the separate arrivals and departures of the two parents together with the behaviours of both chicks in that single moment of time became messy with inaccuracy of the time stamps of the behaviours as all could not be coded at once.

Observations were not subjected to inter-rater reliability testing; all observations and coding were undertaken by the researcher. This may have implications for the reliability of the coding for example, time stamps may not have been accurate and identification of the focal animal and behaviours from the ethogram could have been inconsistent or subject to observer bias. The method of re-coding samples from the pilot study for the full observations revealed that the time stamps and focal animal and behaviour identification for the two sets of observations were the same and therefore had intra-rater reliability. However, this does not allow for scrutiny of any potential observer bias in how the behaviours in the ethogram were interpreted. While the ethogram used motor rather than functional descriptions of each behaviour to ensure objectivity of the interpretation of behaviours, future work in this area would benefit from a sample of observations being coded by an additional researcher to test for inter-rater reliability and observer bias.

Future Directions

The findings of this study provide much scope for future research in this area. Comparisons of the responses of attacked chicks in the Stage 1 age group against productivity of their nests and a repeated measures design tracking them in Stage 3 could elucidate the conditions under which beta chicks will implement appeasement strategies. The difficulty of chick loss during the breeding season would need to be dealt with and again the issue of capturing attacking behaviour. A simpler but similarly revealing study would be to ascertain the prevalence of beta chicks using the facing away+ food gaining strategies within a population and this could be achieved easily with the existing archival footage.

As mentioned above, a formula is certainly needed to get some handle on the rate of chick loss through siblicide and perhaps included in this even filicide. This would help to bring perspective to the behavioural events observed in the nests.

This study did not look at long sequences of behavioural events, but those preceding pecks and following pecks. Reed (2015) used a predefined starting event and tracked the sequence of events that followed. Taking this approach to alpha and beta interactions to determine the broader picture of events leading up to pecking events may be beneficial but would be best done with inclusion of the arrivals and departures of the parent birds and find cues that may have a lag.

Sampling of two-chick nests specifically would be necessary to expand this work. Given the ratio of available films to useable films once criteria had been set for sampling. Building a database of the contents of the films within the archive would be of overwhelming benefit to mining this resource which has fantastic potential for future research on the behavioural repertoires of Kittiwakes.

This study has to my knowledge been the first to apply the use of sequential transition data to Kittiwake interactions and specifically to apply this to sibling chick conflict interactions. There is currently no published literature applying this scheme of analysis to this species and, given the increasing use of these analytical methods in the study of animal behaviour and the detail of interactions that has been revealed by this research, this highlights the use of applying these methods to examining the relationships between Kittiwakes and there is much scope to develop this further. The behavioural repertoires of beta Kittiwake chicks during sibling conflict interactions have been quantified by this research, in particular the strategies beta chicks use to compete for food. As such, knowledge of the behaviours of the *insurance* chick has been broadened. Not least, the findings of the present research expands the documented data for a species in decline. Since sibling conflict is a precursor to brood reduction which in turn affects productivity levels within Kittiwake colonies, the findings and discussion contained in the present study contribute to a broader picture which can inform on the finer detail of Kittiwake chick productivity and suggests directions for future work which may be of benefit in informing conservation efforts.

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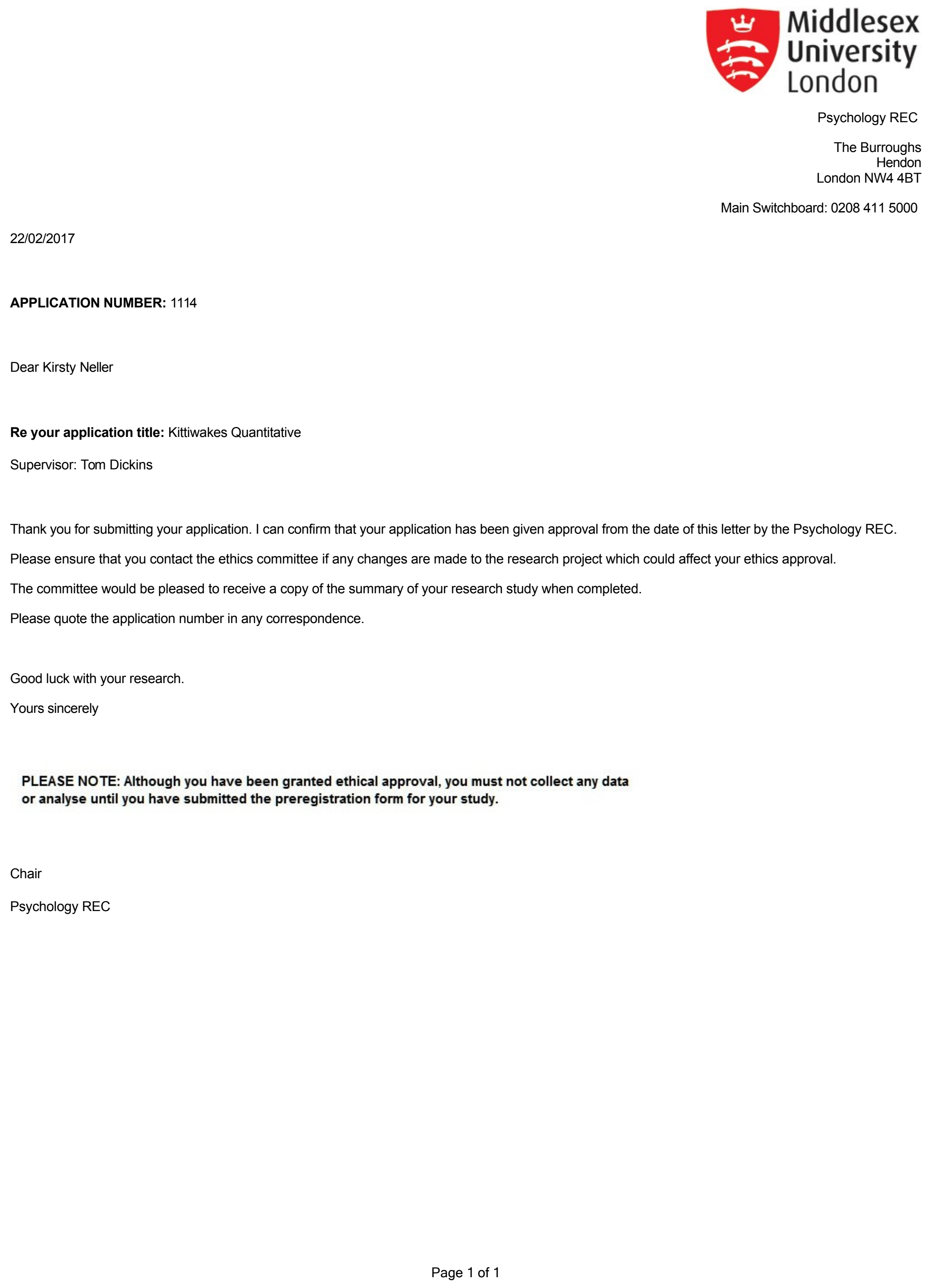
Appendix A

Figure 1: *Hangrybirdometer Predictogram*. Schematic representation used to build the research questions and hypotheses for the current study.



Psychology REC

The Burroughs
Hendon
London NW4 4BT

Main Switchboard: 0208 411 5000

22/02/2017

APPLICATION NUMBER: 1114

Dear Kirsty Neller

Re your application title: Kittiwakes Quantitative

Supervisor: Tom Dickins

Thank you for submitting your application. I can confirm that your application has been given approval from the date of this letter by the Psychology REC.

Please ensure that you contact the ethics committee if any changes are made to the research project which could affect your ethics approval.

The committee would be pleased to receive a copy of the summary of your research study when completed.

Please quote the application number in any correspondence.

Good luck with your research.

Yours sincerely

PLEASE NOTE: Although you have been granted ethical approval, you must not collect any data or analyse until you have submitted the preregistration form for your study.

Chair

Psychology REC

Page 1 of 1

Figure 2: Letter granting ethics approval for application number 1114.

Middlesex University London

Psychology REC

The Burroughs
Hendon
London NW4 4BT

Main Switchboard: 0208 411 5000

08/07/2022

APPLICATION NUMBER: 1114

Dear Kirsty Neller and all collaborators/co-investigators

Re your application title: Kittiwakes Quantitative

Supervisor:

Co-investigators/collaborators: Prof. Tom Dickins

Thank you for submitting your application. I can confirm that your application has been given APPROVAL from the date of this letter by the Psychology REC.

The following documents have been reviewed and approved as part of this research ethics application:

Document Type	File Name	Date	Version
Amendments	Letter	22/02/2017	1

Although your application has been approved, the reviewers of your application may have made some useful comments on your application. Please look at your online application again to check whether the reviewers have added any comments for you to look at.

Also, please note the following:

1. Please ensure that you contact your supervisor/research ethics committee (REC) if any changes are made to the research project which could affect your ethics approval. There is an Amendment sub-form on MORE that can be completed and submitted to your REC for further review.

2. You must notify your supervisor/REC if there is a breach in data protection management or any issues that arise that may lead to a health and safety concern or conflict of interests.

3. If you require more time to complete your research, i.e., beyond the date specified in your application, please complete the Extension sub-form on MORE and submit it your REC for review.

4. Please quote the application number in any correspondence.

5. It is important that you retain this document as evidence of research ethics approval, as it may be required for submission to external bodies (e.g., NHS, grant awarding bodies) or as part of your research report, dissemination (e.g., journal articles) and data management plan.

6. Also, please forward any other information that would be helpful in enhancing our application form and procedures - please contact MOREsupport@mdx.ac.uk to provide feedback.

Good luck with your research.

Yours sincerely,

Chair

Psychology REC

Figure 3: Letter extending ethics approval to Amanda Mead for the current research for application number 1114.

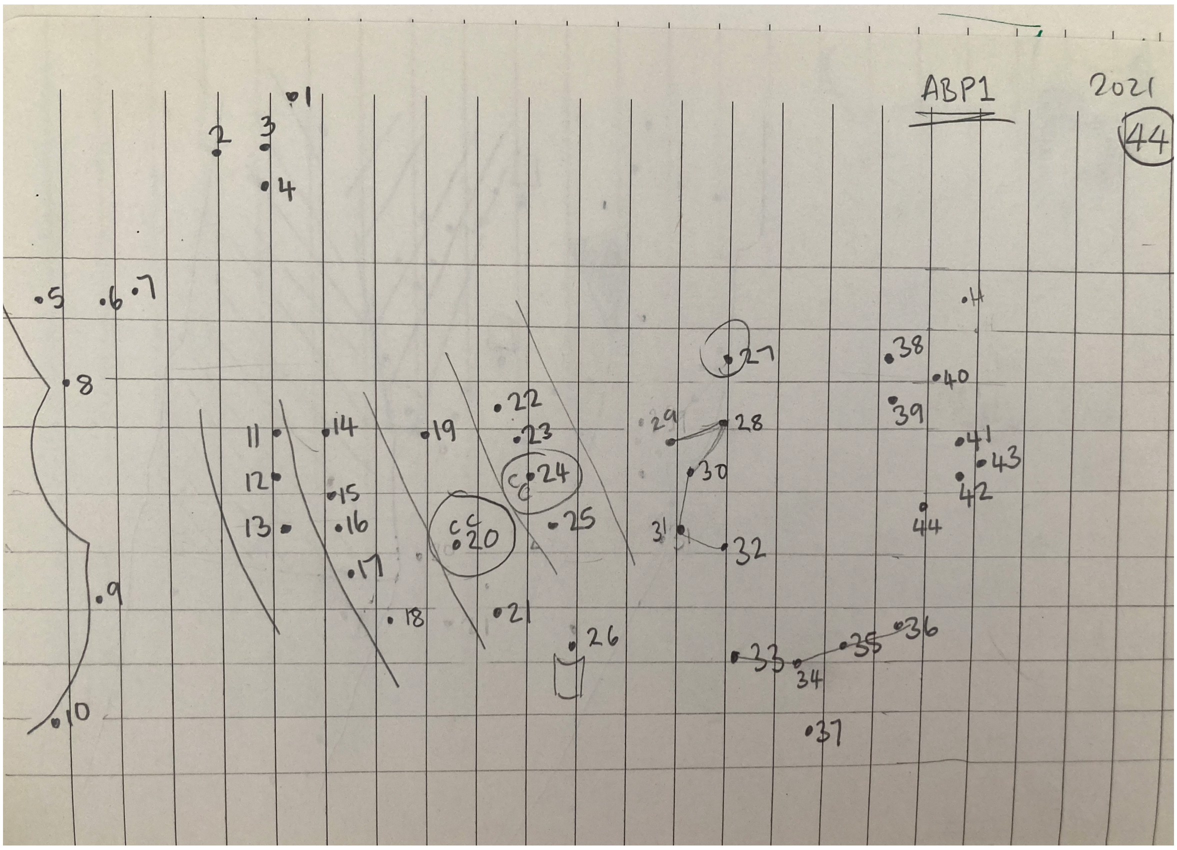


Figure 4: Hand-drawn colony map of ABP1 created during 2021 field study.

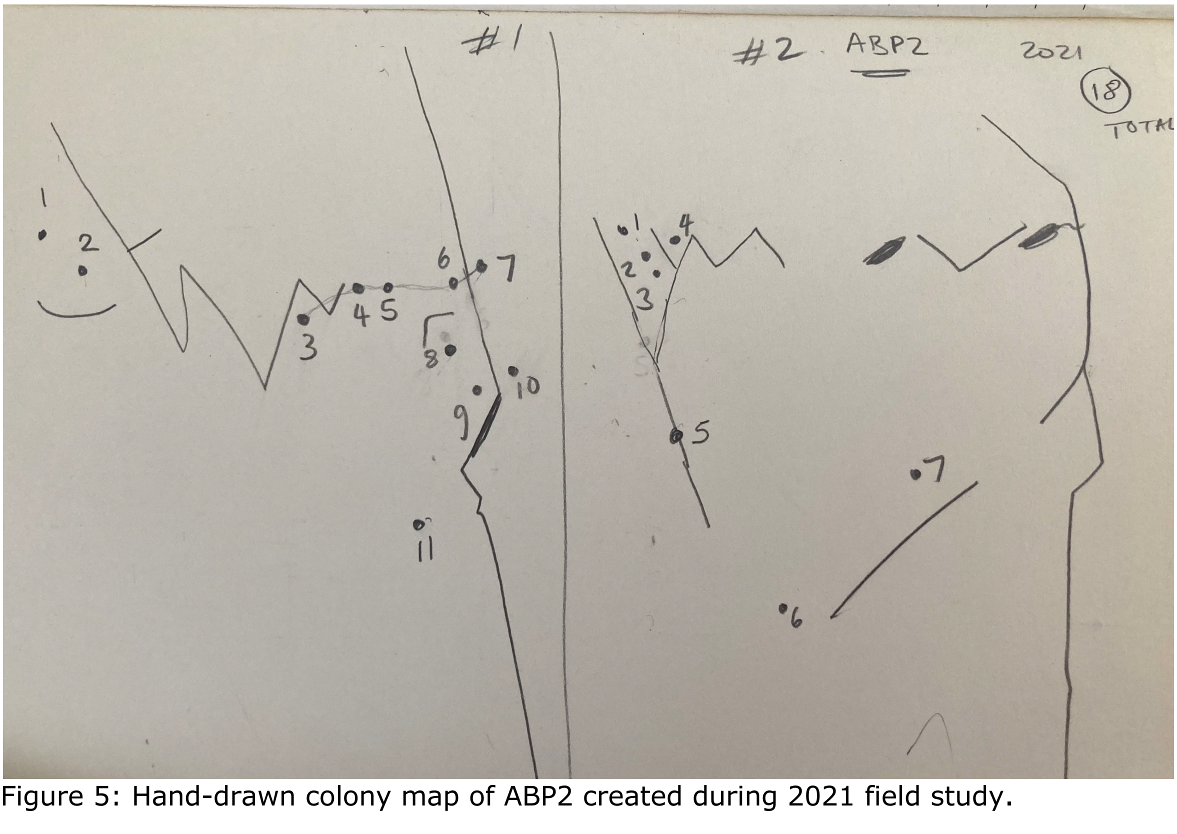


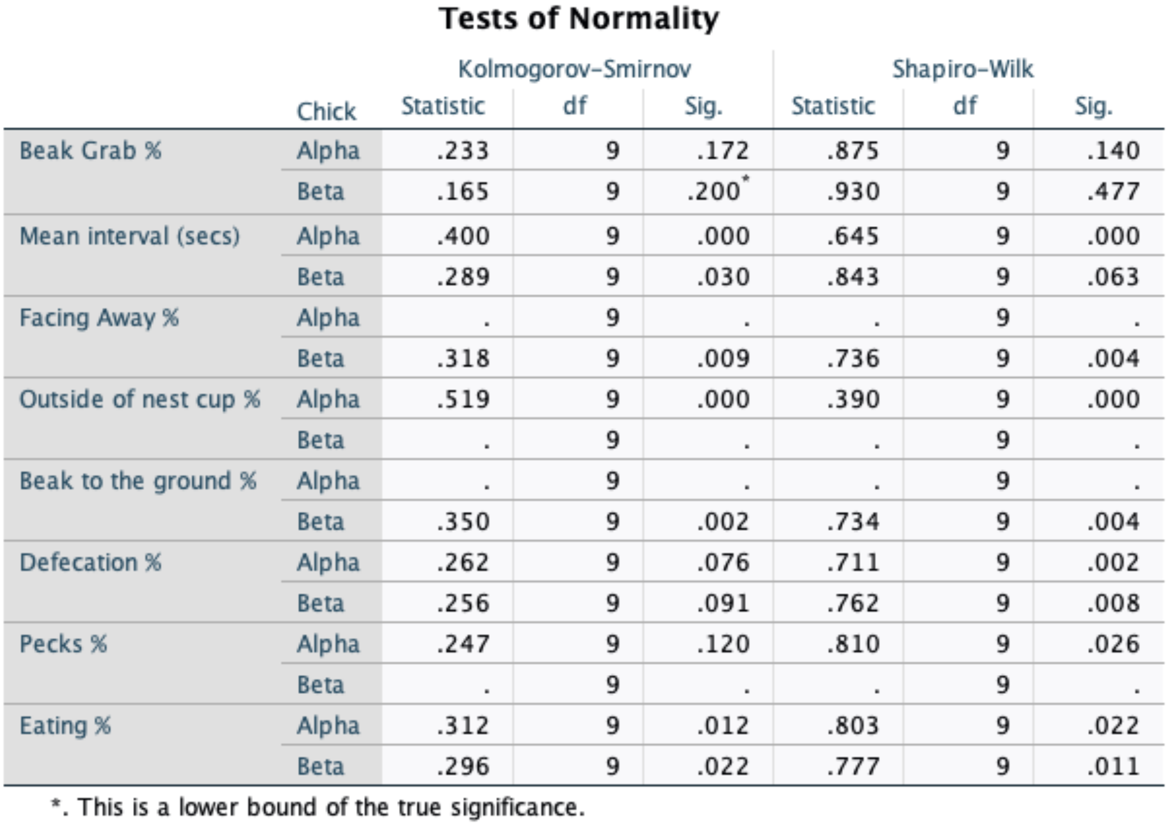
Figure 5: Hand-drawn colony map of ABP2 created during 2021 field study.

Figure 6: Hand-drawn colony map of ABP3 created during 2021 field study.

Appendix B

Inferential testing outputs from SPSS

Table 1: SPSS output displaying results of a Shapiro-Wilk Test of normality for sibling groups.

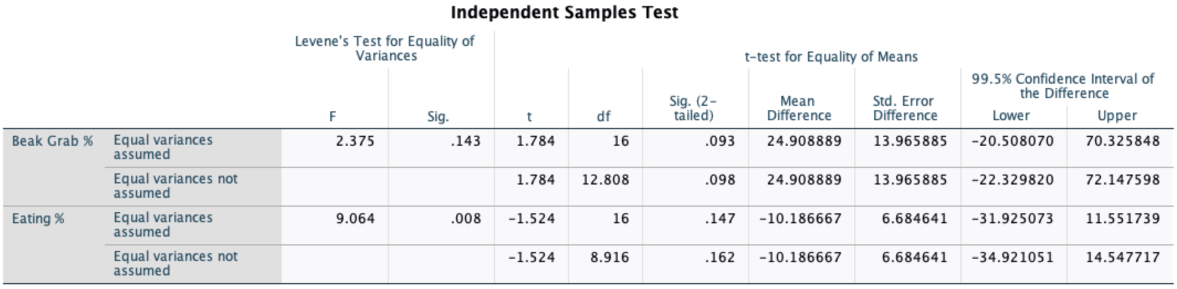


Tests of Normality

		Kolmogorov-Smirnov			Shapiro-Wilk		
	Chick	Statistic	df	Sig.	Statistic	df	Sig.
Beak Grab %	Alpha	.233	9	.172	.875	9	.140
	Beta	.165	9	.200*	.930	9	.477
Mean interval (secs)	Alpha	.400	9	.000	.645	9	.000
	Beta	.289	9	.030	.843	9	.063
Facing Away %	Alpha	.	9	.	.	9	.
	Beta	.318	9	.009	.736	9	.004
Outside of nest cup %	Alpha	.519	9	.000	.390	9	.000
	Beta	.	9	.	.	9	.
Beak to the ground %	Alpha	.	9	.	.	9	.
	Beta	.350	9	.002	.734	9	.004
Defecation %	Alpha	.262	9	.076	.711	9	.002
	Beta	.256	9	.091	.762	9	.008
Pecks %	Alpha	.247	9	.120	.810	9	.026
	Beta	.	9	.	.	9	.
Eating %	Alpha	.312	9	.012	.803	9	.022
	Beta	.296	9	.022	.777	9	.011

*. This is a lower bound of the true significance.

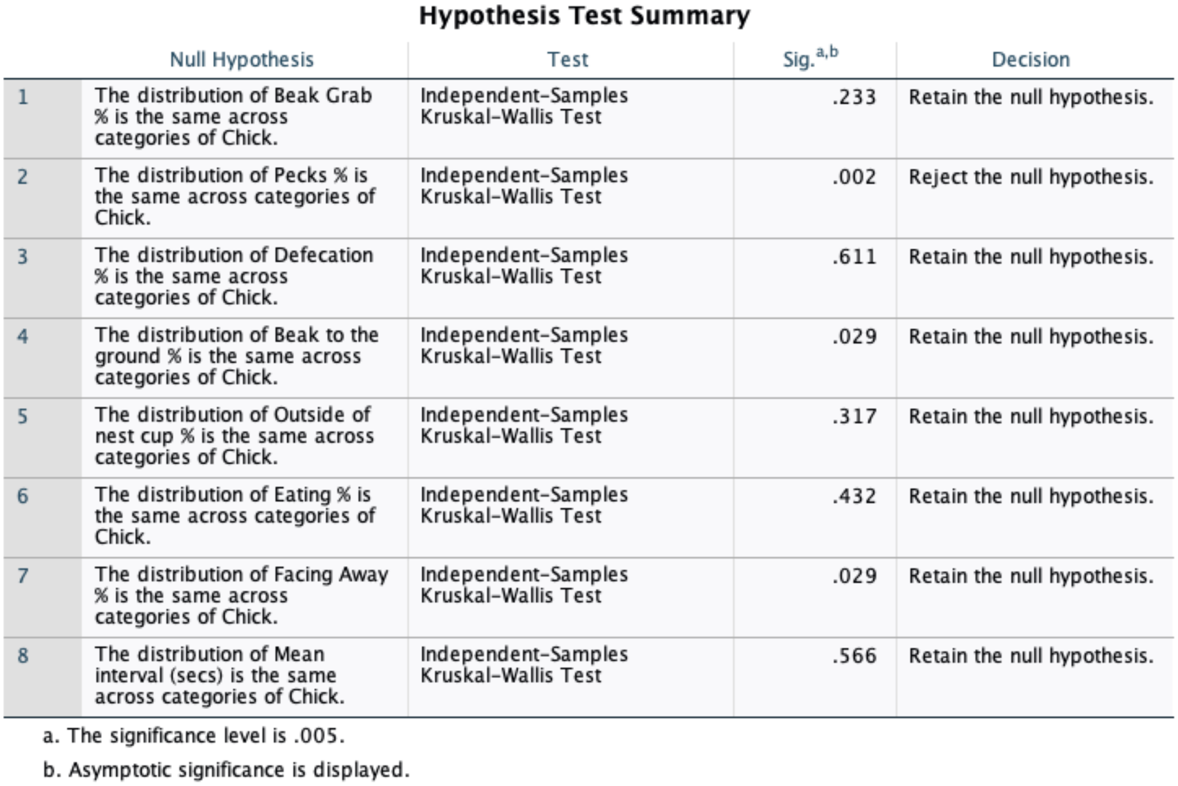
Table 2: SPSS output displaying results of Levene's Tests and t-tests for behaviours with parametric data.



Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									99.5% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Beak Grab %	Equal variances assumed	2.375	.143	1.784	16	.093	24.908889	13.965885	-20.508070	70.325848
	Equal variances not assumed			1.784	12.808	.098	24.908889	13.965885	-22.329820	72.147598
Eating %	Equal variances assumed	9.064	.008	-1.524	16	.147	-10.186667	6.684641	-31.925073	11.551739
	Equal variances not assumed			-1.524	8.916	.162	-10.186667	6.684641	-34.921051	14.547717

Table 3: SPSS output displaying results of Kruskal-Wallis test for distributions of behaviours between sibling groups.



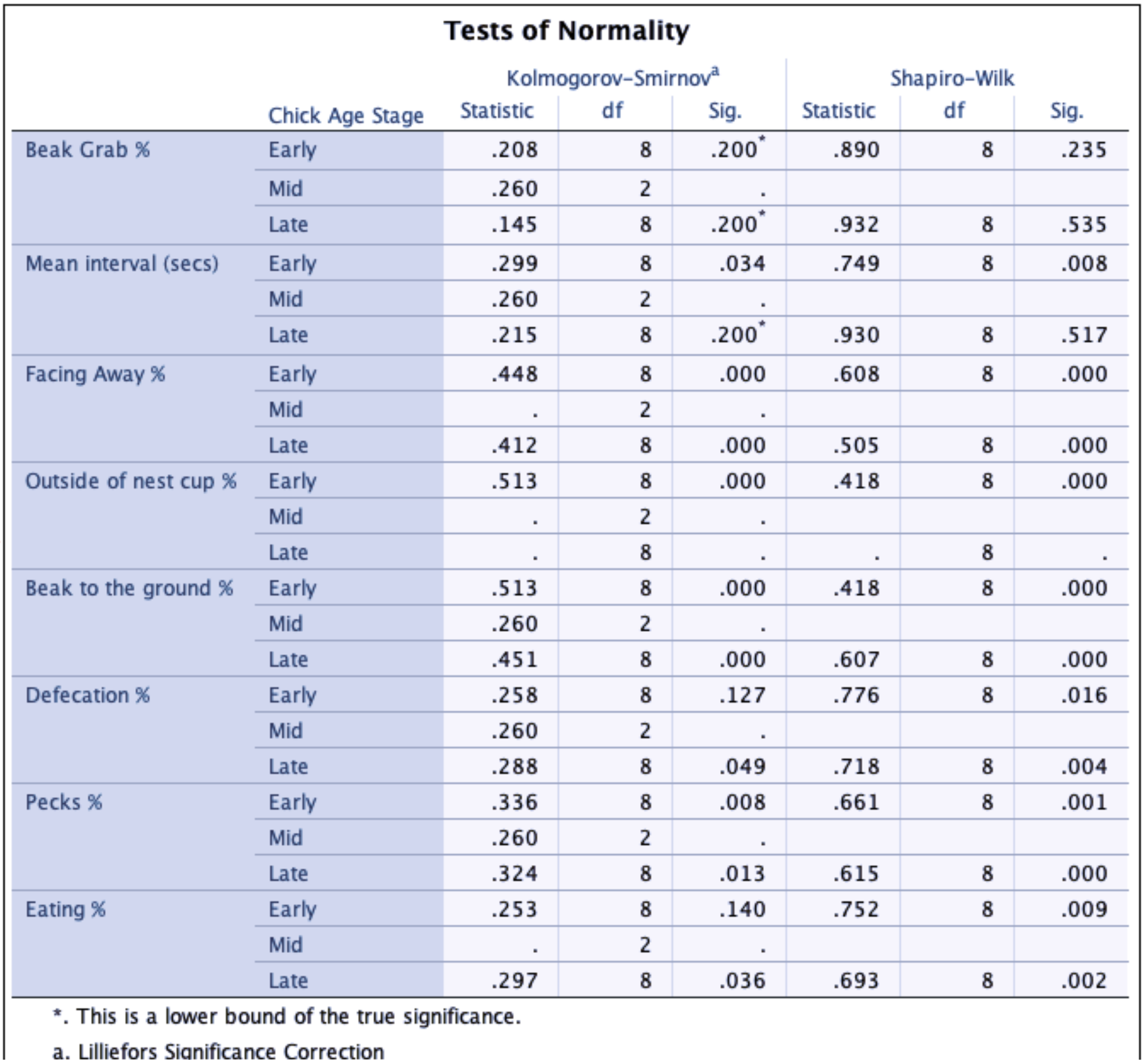
Hypothesis Test Summary

	Null Hypothesis	Test	Sig.[a,b]	Decision
1	The distribution of Beak Grab % is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.233	Retain the null hypothesis.
2	The distribution of Pecks % is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.002	Reject the null hypothesis.
3	The distribution of Defecation % is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.611	Retain the null hypothesis.
4	The distribution of Beak to the ground % is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.029	Retain the null hypothesis.
5	The distribution of Outside of nest cup % is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.317	Retain the null hypothesis.
6	The distribution of Eating % is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.432	Retain the null hypothesis.
7	The distribution of Facing Away % is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.029	Retain the null hypothesis.
8	The distribution of Mean interval (secs) is the same across categories of Chick.	Independent-Samples Kruskal-Wallis Test	.566	Retain the null hypothesis.

a. The significance level is .005.

b. Asymptotic significance is displayed.

Table 4: SPSS Output Shapiro-Wilk test of normality across age stage.



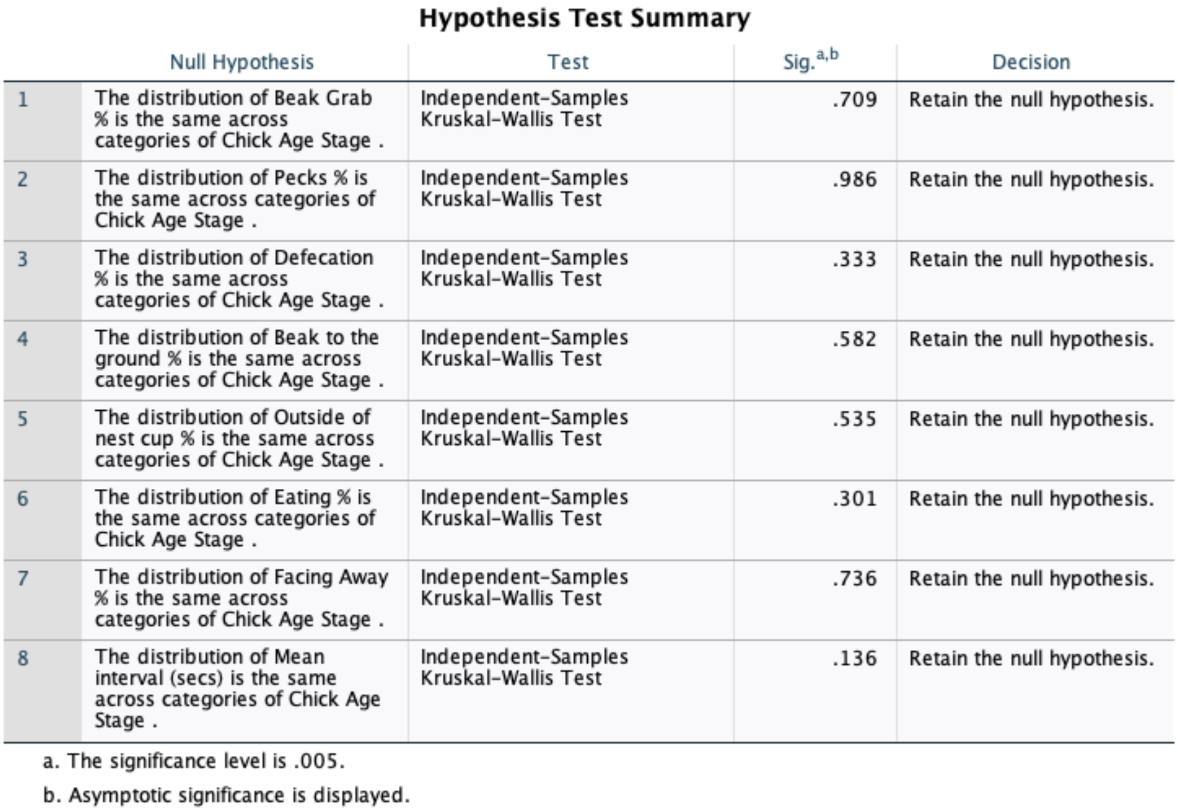
Tests of Normality

		Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Chick Age Stage	Statistic	df	Sig.	Statistic	df	Sig.
Beak Grab %	Early	.208	8	.200*	.890	8	.235
	Mid	.260	2	.			
	Late	.145	8	.200*	.932	8	.535
Mean interval (secs)	Early	.299	8	.034	.749	8	.008
	Mid	.260	2	.			
	Late	.215	8	.200*	.930	8	.517
Facing Away %	Early	.448	8	.000	.608	8	.000
	Mid	.	2	.			
	Late	.412	8	.000	.505	8	.000
Outside of nest cup %	Early	.513	8	.000	.418	8	.000
	Mid	.	2	.			
	Late	.	8	.	.	8	.
Beak to the ground %	Early	.513	8	.000	.418	8	.000
	Mid	.260	2	.			
	Late	.451	8	.000	.607	8	.000
Defecation %	Early	.258	8	.127	.776	8	.016
	Mid	.260	2	.			
	Late	.288	8	.049	.718	8	.004
Pecks %	Early	.336	8	.008	.661	8	.001
	Mid	.260	2	.			
	Late	.324	8	.013	.615	8	.000
Eating %	Early	.253	8	.140	.752	8	.009
	Mid	.	2	.			
	Late	.297	8	.036	.693	8	.002

*. This is a lower bound of the true significance.

a. Lilliefors Significance Correction

Table 5: SPSS output for Kruskal-Wallis test for distributions of behaviours between age stage.



Hypothesis Test Summary

	Null Hypothesis	Test	Sig.^{a,b}	Decision
1	The distribution of Beak Grab % is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.709	Retain the null hypothesis.
2	The distribution of Pecks % is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.986	Retain the null hypothesis.
3	The distribution of Defecation % is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.333	Retain the null hypothesis.
4	The distribution of Beak to the ground % is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.582	Retain the null hypothesis.
5	The distribution of Outside of nest cup % is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.535	Retain the null hypothesis.
6	The distribution of Eating % is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.301	Retain the null hypothesis.
7	The distribution of Facing Away % is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.736	Retain the null hypothesis.
8	The distribution of Mean interval (secs) is the same across categories of Chick Age Stage .	Independent-Samples Kruskal-Wallis Test	.136	Retain the null hypothesis.

a. The significance level is .005.

b. Asymptotic significance is displayed.

Appendix C

BORIS Behavioural String Output

Below is the entire output from the behavioural observations from the BORIS software. Preceding each string is the observation ID, along with the age stage of chicks in the observation, and any additional information such as an identifier where there was more than one nest in the film footage.

These strings were generated by BORIS and exported. They were then imported into Behatrix for analysis.

```
# Media file name: ABP1 #8_8 JUL 2018.mp4
# Year: 2018
# Chick Age Stage: 1
# Plot: ABP1
# Nest Number: 1

[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Eating|[Alpha]Eating|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Eating|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Eating|[Alpha]Beak Grab|[Beta]Beak
Grab|[Beta]Eating|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Beta]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Eating|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Beta]Facing
away|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Facing away|[Alpha]Eating|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Beta]Facing
away+Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Beta]Facing away+Beak Grab|[Beta]Facing away+Eating|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Defecation|[Beta]Facing
away+Defecation
```

```
# Media file name: ABP1 #1_8 JUL 2018.mp4. Left nest.
# Year: 2018
# Chick Age Stage: 1
# Plot: ABP1
# Nest Number: 1

[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab
```

```
# observation id: ABP1  2_8 JUL 2018 LEFT NEST View A
# Year: 2018
# Chick Age Stage: 1
# Plot: ABP1
# Nest Number: 1

[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Beak Grab

# observation id: ABP1  3_8 JUL 2018.  LEFT NEST
# Year: 2018
# Chick Age Stage: 1
# Plot: ABP1
# Nest Number: 1

[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Beta]Beak to the
ground|[Alpha]Beak Grab

# observation id: ABP1  5_8 JUL 2018
# Year: 2018
# Chick Age Stage: 1
# Plot: ABP1
# Nest Number: 1

[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Beta]Beak Grab|[Alpha]Outside of nest cup|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Defecation|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Defecation

# observation id: ABP1  7_8 JUL 2018 BOTTOM RIGHT
# observation description: Same nest as in ABP1 8_8 JUL 2018
# Year: 2018
# Chick Age Stage: 1
# Plot: ABP1
# Nest Number: 1
```

```
# observation id: ABP1  9_8 JUL 2018
# Year: 2018
# Chick Age Stage: 1
# Plot: ABP1
# Nest Number: 1

[Beta]Facing away|[Alpha]Defecation|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Beta]Beak Grab|[Alpha]Peck|[Beta]Facing away|[Alpha]Beak
Grab|[Alpha]Eating|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Facing
away|[Beta]Beak Grab|[Beta]Eating|[Beta]Facing
away|[Beta]Eating|[Beta]Eating|[Beta]Eating|[Beta]Eating|[Alpha]Peck|[Beta]Facing
away|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alph
a]Peck|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Eating|[Beta]Eating|[Beta]Facing
away|[Beta]Eating|[Alpha]Peck|[Beta]Facing away|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak
Grab|[Beta]Eating|[Beta]Facing
away|[Alpha]Eating|[Beta]Eating|[Beta]Eating|[Beta]Eating|[Alpha]Peck|[Beta]Facing
away|[Beta]Eating|[Alpha]Peck|[Beta]Facing away|[Beta]Eating|[Beta]Facing
away|[Beta]Eating|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Beak
Grab|[Beta]Eating|[Alpha]Peck|[Beta]Facing away|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Beak
Grab|[Beta]Eating|[Alpha]Eating|[Beta]Eating|[Beta]Eating|[Alpha]Eating|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab

# observation id: ABP1 N17, 18, 20 (1) 12_07_2021
# observation description: Focus on nest 17 (TOP LEFT) STAGE 3 chicks
# Year:  2021
# Chick Age Stage:  3
# Plot: ABP1
# Nest Number: 17

[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Beak
Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Defecation|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab

# observation id: ABP1 N17, 18, 20 (3) 12 July 2021
```

observation description: Focus on Nest 17. This is the 3rd follow on video on the same day of nest 17.
Year: 2021
Chick Age Stage: 3
Plot: ABP1
Nest Number: 17

[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab

observation id: ABP1 N17,18,20 (2) 12_07_2021
observation description: Nest 17. Video 2 of 3.
Year: 2021
Chick Age Stage: 3
Plot: ABP1
Nest Number: 17

[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab

observation id: ABP1 N38 (1)-1 10_07_2021
observation description: Video 1 of 2
Year: 2021
Chick Age Stage: 2
Plot: ABP1
Nest Number: 38

[Beta]Defecation|[Beta]Defecation|[Alpha]Defecation|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Defecation|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Defecation|[Alpha]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab

observation id: ABP1 N38 (2)-1 10_07_2021
observation description: Follow on video from ABP1 N38 (1)-1 10_07_2021 STAGE 2 chicks
Year: 2021
Weather: Sun
Chick Age Stage: 2
Plot: ABP1
Nest Number: 38

[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Peck|[Alpha]Peck|[Beta]Beak to the ground|[Alpha]Beak Grab

observation id: ABP1 Nests 17_18_22 (1) 20_JUL_2019 TOP LEFT
observation description: Top left nest. STAGE 3 chicks
Year: 2019
Chick Age Stage: 3
Plot: ABP1
Nest Number: 1

[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Eating|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab

observation id: ABP1 Nests 17_18_22 (2) 20_JUL_2019 TOP LEFT
observation description: Video 2 o3 3 of the top left nest. STAGE 3 chicks
Year: 2019
Chick Age Stage: 3
Plot: ABP1
Nest Number: 1

[Beta]Facing away|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Beak

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Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab

# observation id: ABP1 Nests 17_18_22 (3) 20_JUL_2019 TOP LEFT
# observation description: Video 3 of 3, top left nest.  STAGE 3 chicks.
# Year:  2019
# Chick Age Stage:  3
# Plot: ABP1
# Nest Number: 1

[Beta]Facing away|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Eating|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab

# observation id: ABP2 Nest 12_11_10_7 (2) 20_JUL_2020.mp4
# observation description: Right nest
# Year: 2018
# Chick Age Stage:  3
# Plot:  ABP2
# Nest Number: 1

[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Beta]Beak Grab|[Beta]Eating|[Beta]Beak Grab|[Beta]Beak
Grab|[Beta]Beak Grab|[Beta]Beak Grab|[Beta]Eating|[Beta]Defecation|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Eating|[Alpha]Peck|[Beta]Beak to the ground|[Alpha]Beak
Grab|[Alpha]Beak Grab|[Alpha]Defecation

# observation id: ABP3 Nests 14_15_13_11 (1) 22_JUL_2019
# observation description: Video 1 of 3. Only 1 2chick nest.  STAGE 3 chicks
# Year: 2018
# Chick Age Stage:  3
# Plot:  ABP3
# Nest Number: 1


# observation id: ABP3 Nests 14_15_13_11 (2) 22_JUL_2019
# observation description: There is only 1 2chick nest in this vid.  This is vid 2 of 3.
STAGE 3 chicks
# Year:  2019
# Chick Age Stage:  Near to fledging
# Plot:  ABP3
# Nest Number: 1

[Beta]Facing away|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha
]Peck|[Alpha]Peck|[Alpha]Eating|[Beta]Eating|[Beta]Facing
away|[Alpha]Peck|[Beta]Eating|[Alpha]Peck|[Beta]Facing away|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Beak
Grab|[Alpha]Eating|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak
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Grab|[Alpha]Beak Grab|[Beta]Eating|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Beta]Eating|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Beak Grab|[Beta]Eating|[Alpha]Beak Grab|[Alpha]Beak Grab|[Alpha]Peck|[Beta]Eating|[Alpha]Beak Grab|[Alpha]Peck|[Alpha]Beak Grab|[Beta]Eating|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Alpha]Peck|[Beta]Beak to the ground|[Alpha]Defecation|[Alpha]Defecation

observation id: ABP3 Nests 14_15_13_11 (3) 22_JUL_2019
observation description: Video 3 of 3. Only 1 2chick nest. STAGE 3 chicks
Year: 2019
Chick Age Stage: 3
Plot: ABP3
Nest Number: 1

[Alpha]Eating|[Beta]Eating|[Alpha]Eating|[Alpha]Peck

observation id: Aztec Bay (1) June 2021 ABP3
Year: 2021
Chick Age Stage: 1
Plot: ABP3
Nest Number: 1

[Alpha]Eating

observation id: Aztec Bay (3) June 2021 ABP1 20
Year: 2021
Chick Age Stage: 1
Plot: ABP1
Nest Number: 20

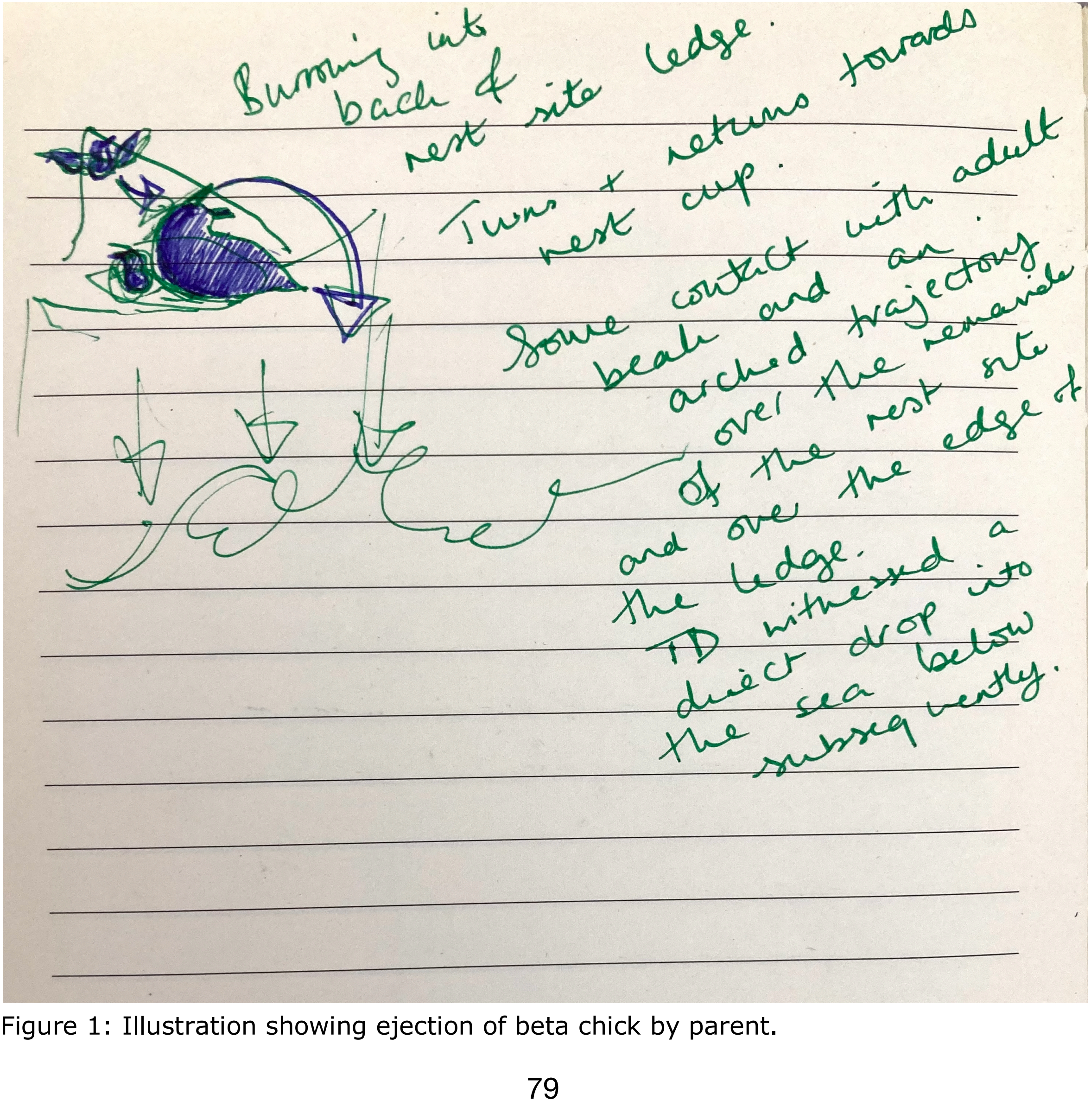
observation id: Aztec Bay (8) June 2021 ABP3
Year: 2021
Chick Age Stage: 1
Plot: ABP3
Nest Number: 1

Appendix D

Field notes from June 2021 site visit to Lundy

Nest surveys through the duration of the period 14th-18th June recorded a number of 2 chick nests across the Aztec Bay colony. Chick loss occurred from nests in ABP1 but no loss occurred from 2-chick nests. These losses were presumed a consequence of predation due to sightings of prospecting (lesser or greater) black backed gulls. No 3-chick nests were recorded within the colony during the June surveys.

Beta chick in ABP1 Nest 24 lost on 17th June at time and the sequence of events of this loss are documented and discussed by witnesses (myself and Tom Dickins) in detail. A scan of the colony detected unusual movement in Nest 24. The beta chick was observed away from the nest cup and was facing into the back corner of the nest ledge. The nest site was such that the floor of the site extended well beyond the nest cup, allowing for movement beyond the nest cup. The chick, which from previous days' surveys was known to be one day old appeared to be moving its wings rapidly and pressing repeatedly into the wall corner. Preceding events are unknown. After some minutes the chick turned and wandered back towards the nest cup. At this point the chick came up against the parent bird at which point it appeared to be briefly in contact with the parent's beak and was flung in an upwards arch on a trajectory across the remaining distance from its position across the edge of the nest and into the sea below (Figure 1).



Burrowing into back of nest site ledge.

Turns + returns towards nest cup.

Some contact with adult beak and an arched trajectory over the remainder of the nest site and over the edge of the ledge.

TD witnessed a direct drop into the sea below subsequently.

Figure 1: Illustration showing ejection of beta chick by parent.