Can parental investment reduce social altruistic behaviour in Yellow-legged Gulls *Larus michahellis*?

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Abstract

This study aims to test if there are differences in nest defence behaviour in single and in groups of Yellow-legged Gulls *Larus michahellis* during two stages of the breeding season: incubation and early chick-rearing period. When a human intruder wearing a mask approached and stood still next to the target nest during incubation, the gulls took part in passive mobbing and helped the 'attacked' gull, thereby showing altruistic behaviour. In contrast, during the early chick-rearing period, decreased altruistic behaviour was observed: the individuals that took part in the passive mobbing tended to remain on their own nests, in order to look after their own chicks. In this stage, a reduction of the size of passive mobbing was also noted. Furthermore, gulls from disturbed nests increased the intensity of nest defence by increasing the number of dives directed at the heads of the human intruders. Again, those gulls whose nests were directly affected by an approaching human intruder left their nests quickly to begin an aerial defence, encouraging the chicks to leave the nest and hide among rocks and shrubs. The adult gulls came back to their nests only after the danger had ceased and the chicks had come back to their nests, in agreement with the Parental Investment Theory.

Introduction

Coloniality in nesting birds represents an important life-history strategy to maximize reproductive success (Herring & Ackerman 2011). Efficient anti-predator behaviour is crucial for the survival of animals (Lima & Dill 1990; Graw & Manser 2007). In this context, nest defence has been studied in a large number of bird species as an example of anti-predator behaviour (e.g. Kruuk 1964; Shields 1984; Sibley & McCleery 1985; Stone & Trost 1991). The reduction of predation risk through direct defence by group members has been suggested to play a primary role in group survival (Kazama & Watamuki 2011). The animals that vigorously defend against predators may experience a decrease in predation risk (Dugatkin & Gudin 1992). When colonial nesting birds are threatened by predators, group mobbing or attacks reduce nest predation risk by chasing the predator away (Montevecchi 1979; Whittam & Leonard 2000).

In fact, many animals display increased risk-taking behaviour during the mating season resulting in increased reproductive success (e.g. Kruuk 1964; Horn 1968; Dill *et al*. 1999; Berzins *et al*. 2010). Mobbing has been well documented in a variety of animals and this conspicuous anti-predator strategy quickly recruits both conspecifics (Anderson & Wiklund 1978; Krams *et al*. 2010) and heterospecifics (Hurd 1996; Krams & Krama 2002).

However, mobbing behaviour has some costs including risks of injury and death to the mobber (Poiani & Yorke 1989) as well as a waste of time and energy (Collias & Collias 1978). Several studies have documented an increase in time in mobbing as a part of nest defence during the breeding period. In contrast, mobbing may be rarely performed either during nest building or in the egg-laying phase (Montgomerie & Weatherhead 1988; Redondo 1989). Theoretical models and life-history evolution predict that in resolving the parental dilemma, an animal's decision on whether to take care of themselves or of their offspring depends on the offspring value and their own probability of survival (Trivers 1971, 1974; Anderson *et al*. 1981; Redondo 1989; Berzins *et al*. 2010). Parents can increase their fitness by investing more in older rather than young offspring, which explains the increase in the intensity of mobbing as the breeding season advances (Carlisle 1985; Montgomerie & Weatherhead 1988). Moreover, mobbing often includes swoops at a potential predator and it may involve direct attack, with physical contact made by the mobber (e.g. Hartley 1950; Kruuk 1964; Gramza 1967; Curio 1978). The notion of mobbing as parental care implies that it will reduce the predation rate on the mobber's progeny (Greig-Smith 1980; Biermann & Robertson 1982). If this is true, mobbing would provide direct benefits by increasing the reproductive portion of the personal component of the mobber's inclusive fitness (Brown & Brown 1981; Shields 1984) as the primary beneficiaries of mobbing are the offspring (Shields 1984).

When a predator or an intruder steps into a breeding colony of gulls, animals near to it fly off performing alarm calls. Alarm calls alert other individuals that fly off and join the other birds. This group flies in a circle round the predator and some animals, normally the owners of the directly threatened nests, perform dives against the predator or intruder (Shields 1984). Dives are flights starting from the sky in the direction of the predator's head, usually without contact. Subjects performing dives against the predator are called 'active mobbers' and the meaning of this behaviour is an active offspring defence. Active mobbing is directly involved with nest defence and is measured by the number of gulls flying high and around the head of the intruder. Passive mobbers are a random sample of the local population (Shields 1984). If passive mobbers leave the nest, they face an increased risk of their chicks being preyed on by other predators. From a merely adaptive point of view, passive mobbing is apparently profitless.

Passive mobbing is usually less risky than active mobbing, but the costs of becoming a passive mobber include an energetic and time cost as well as an increased risk of personal injury due to mid-air collisions with other gulls (Conover 1987). Moreover, other gulls are potentially dangerous predators of gull chicks. Cannibalism is a frequent behaviour in gulls (Burger & Gochfeld 1985). Kruuk (1964, 1976), Curio (1978), Shields (1984), Conover (1987) and Ostreiher (2003) have proposed an interpretation of the adaptive value of passive mobbing; this circular flight aims to frighten and 'study' the intruder to evaluate its level of danger (e.g. predator of adults, predator of chicks, predator of eggs, where it comes from), study its strategies of attack and so on. Obviously, predators of adult animals are considered the most dangerous. Therefore, passive mobbing has a social purpose. In fact, the intruder can be frightened by a large number of gulls flying and making alarm calls above its head. Once the gulls have studied the intruder, they go back to their nests (Kruuk 1976; Curio 1978; Conover 1985). Accordingly, researchers usually divide the period of exposition to intruders into sub-periods in order to observe the decrease of mobbing animals (habituation to the human).

Parental investment reflects the effort that parents make to increase the survival of their offspring as a trade-off with their own future prospect of survival and reproduction (Trivers 1974). Studies of parental investment suggest that individual parents are consistent in the intensity of their defence of offspring within and among reproductive events (Montgomery & Weatherhead 1988). The intensity with which parents defend their offspring, and the risk they expose themselves to, should reflect the reproductive value (Fisher 1930; Williams 1966). The intensity of defence of offspring peaks at an intermediate age (2 years) followed by decrease into old age and senescence (Møller & Nielsen 2014). Several researchers developed the Parental Investment Theory (Trivers 1971, 1974; Dawkins & Carlisle 1976; Maynard Smith 1977). Parental investment behaviour is related to the mating system (monogamy and polygamy) and the characteristics of offspring (age, vulnerability, quality, number). This theory accounts for the seasonal trend in the defensive behaviour by assuming an increasing value of the offspring for the parents during the rearing season (Siderius 1993). Therefore, both male and female adults defend chicks with increasing intensity during their growth (Jones *et al*. 2002). Several authors studied the risk run by parents during nest defence (Fisher 1930; Williams 1966; Møller & Nielsen 2014). In this context, some studies show an increasing nest defence behaviour with the age of offspring. Montgomerie & Weatherhead (1988) suggested that the nest defence should increase with offspring age because they become more valuable to their parents. According to these authors, the intensity of defence should increase gradually as long as the probability that eggs will hatch increases. The intensity of nest defence should decrease as soon as chicks are able to defend themselves from predators. Knight & Temple (1986) suggested that this change in nest defence with the age of offspring depends on the experimental situation. According to these authors, the increase in offspring value during the first period of life may depend on two different reasons: (i) replacing an older offspring with a new brood is more expensive than replacing a younger one (Barash 1975); (ii) the probability of a successful nest-building decreases as the season progresses (Buitron 1983).

Framed into these theoretical and experimental contexts, this research aims to study the modifications of nest defence behaviour in relation to two different reproductive sub-periods: incubation (from two weeks after the egg is laid) and early chick rearing (from one to three days after hatching). Different behaviours were measured for individuals and groups. In the case of single gulls, the following behaviours were measured: (i) alert; (ii) escape; (iii) flight, with a human intruder approaching, or staying still beside the target nest; (iv) landing and (v) return to the nest with a human intruder going away from the target nest. Moreover, active mobbing in parents from the target nest was measured with the human intruder staying still beside the nest.

In the case of groups, the size of passive mobbing was measured with a human intruder staying still beside the target nest.

From a methodological point of view, this study follows an ethological approach combined with a typical experimental set up under laboratory conditions. In this line, the human intruder operated under strictly controlled conditions: the step pace while approaching the nest as well as the distance and the position of the human intruder from the target nest during a two-minute stay beside the nest. In this experimental approach, a strict control of variables as well as the internal validity were guaranteed by randomizing the following variables: trials, target gulls, days and time of the day. Likewise, external validity was guaranteed by studying the animals in their own habitat during the reproductive period.

Methods

Study area: This study was carried out at Piana Island (39°11’29’’N, 8°19’14’’E), a small island between Stintino and Asinara Island in Northern Sardinia, Italy (Figure 1). Two different reproductive sub-periods were considered: incubation (from 20 March to 7 April 2015) and early chick rearing (from 20 April to 15 May 2015). Across the island there is a large colony of Yellow-legged Gulls *Larus michahellis* homogeneously distributed. Observations were performed in an area about 600 m x 800 m wide. The flat surface and the presence of shrubs allow behavioural observations as well as camouflaging with negligible interference with the gulls’ usual activities. The gulls have no predators on the island. Furthermore, there is a great deal of available food due to a municipal dump in Porto Torres, a small city about 10 km away from Piana Island. The gulls’ nesting area is located in a 2,000 m^2 wide U-shaped zone surrounded by the sea (Figure 1).

Subjects: The whole colony was made up of about 500 nests of Yellow-legged gulls, but in the experimental area there were 73 nests. The experimental subjects were selected among the ones whose nests were located at the edge of the strip in order to facilitate the approach by a human intruder. A second criterion of choice was the distance between nests in order to avoid repeated disturbances due to the experimental procedure: nests were at least 4 m apart from the next nearest nest (mean = 6 m, SD = 3 m). The target nests were tested every day from 10.00 hours until 18.00 hours. In a day, each nest was tested only once and every test was carried

Figure 1. Piana Island and the experimental area. The square is the researchers' standby place. The dot is the fixed camera position.

out after 35–50 minutes from the previous one in order to wait for complete silence again after the human intruder had left. Hence, gulls were not disturbed in their usual activities. The experimental period was from 20 March to 15 May 2015. Nevertheless, only 33 days were spent on the island to carry out the experiment owing to unfavourable weather conditions restricting the observations (e.g. rain, wind, air temperature lower than 18°C). Air temperature is an important factor to consider as it influences mating and hatching; for example, hatching is delayed at air temperatures lower than 18°C (Burger & Gochfeld 1985). The mean date of egg-laying was 27 February 2015 (SD = 10 days).

Subjects from the selected nests were tested twice: once during the incubation period (47 subjects) and once during the chick-rearing period (23 subjects). The reduction in numbers was due to high mortality of chicks and cannibalism of chicks by other adult gulls.

To minimise observer bias, blinded methods were used when all behavioural data were recorded and analysed. During the first two days on the island the equipment was tested to optimise position and distance for the video cameras. Moreover, some preliminary experiments were performed to set the most effective experimental procedure (e.g. number of steps to take from the starting point to the nest, walking pace etc.). The choice of nests was another important preliminary step. The selection criteria were: a) a minimum of two eggs; b) no cracked or hatched eggs; c) easy access; d) vegetation not interfering with visibility of the gulls of the studied nest. Each nest was assigned a reference letter and its position drawn on a map. The starting point for the approach and the position of the video camera were specific for each nest.

Stimuli: A 'human intruder', always the same person to avoid any bias, walked towards the subject wearing a mask with two human eyes drawn on it (Figure 2). The mask allowed for the presentation of a standardised stimulus to the gull on the nest. In order to minimise the contrast between the human intruder's face and the mask itself, the mask was covered with a beauty product to mimic the complexion of the wearer's face.

Figure 2. The human intruder wearing the experimental stimuli with drawn on eyes.

Experimental conditions: Testing was carried out between 10.00 hours and 18.00 hours in order to perform observations under similar light conditions. Testing was randomised according to the time of the day to avoid circadian effects. An interval of about 40 minutes was used between tests to avoid habituation. Air temperature, wind speed and direction were recorded using an analogic thermometer and an anemometer, respectively, for each test. The experiment was interrupted during three days with strong wind, heavy rain or air temperature lower than 18°C to avoid any interference with the usual life in the colony and minimise the dangers for gulls and eggs.

Pre-experiment: During the days before the experiment, the following preliminary activities without data collection were performed: (1) the researchers were dressed with camouflage clothes to minimise the impact on the colony; (2) during the first two days the researchers stood in the experimental site making minimal movements to enable the gulls to get used to their presence. During this preliminary phase, the parents did not leave the tested nests. Likewise, while the researchers were present, no gull stopped incubating and cannibalism was not observed during the pre-experiment.

Experimental procedure: The experimental procedure was standardised for all tests. All the researchers wore brown-green shirts and trousers and squatted on the ground about 40 steps away from the target nests. The researcher playing the role of 'human intruder' squatted with their back turned towards the gull and was positioned at the previously stated starting point. The human intruder wore a mask and earphones. The 47 selected nests were approached by the human intruder in a randomised sequence in two different periods. Hence, each nest was tested twice: once during incubation and once during early chick rearing. A randomised sequence of nest names (e.g. A, C, F, AA, AF,... etc.) specified the order of approach of the human intruder to the selected nests to control for any confounding effects of the sequence of presentation (i.e. neighbourhood of nests, time of day). A metronome, marking 80 beats per minute, was used to standardise the step pace and consequently the speed of approach. After eight seconds, the human intruder stood up and two seconds later walked towards the nest. One of the observers (with video camera) called out to the human intruder the start time for every action in the experimental sequence. At 50 cm from the nest the human intruder stopped for two minutes. Afterwards, they went back to the starting point at the same step pace.

Variables: Two video cameras were used to film the observations, one fixed and the other moving. The fixed video camera was positioned at a standardised distance (35 m from the nest) with constant focal length to obtain a standard framing. In the standard framing the reference point was the nest located at the centre of the lower side of the frame. The standard framing was useful to count the mobbers. The moving video camera tracked the gull from the study nest during its flight to reconstruct the different behaviours from take-off to landing. Two researchers monitored the film to select the different behaviours and identify the beginning of every single behaviour. For example, 'time alert' was referred to as the time spent from the start of the trial until the neck straightening of the gull.
The measures belong to two different types (A and B):

A) escape behaviours (measured in seconds):
- a1 - Alert: first alarm reaction with neck straightening;
- a2 - Flight: fly away from the nest;
- a3 - Landing;
- a4 - Nest: when the gull sits on the nest.

Alert and flight were measured starting from the 'start 1' time. Start 1 time was the moment when the human intruder moved from the starting point. 'Landing' and 'nest' were measured starting from the "start 2" time when the gull left the nest.

B) defence behaviours:

- b1 - Passive mobbing: maximum number of mobbers per interval (all periods of two minutes were divided into six intervals of twenty seconds each);
- b2 - Active mobbing: number of dives (threatening dives made against the intruder).

The number of dives was obtained by counting the dives against the intruder during the two-minute stay of the human intruder near the nest. The mobbing was measured by counting the mean number of mobbers in six subsequent periods of twenty seconds each.

Data analysis: Data were analysed at three different levels. In order to verify differences between incubation and early chick-rearing periods for behaviours a 2 x 4 repeated ANOVA was performed. The first factor was Period (two levels: Incubation and Chick Rearing), the second factor was Behaviours (four levels: Alert, Flight, Landing and Nest). In order to verify differences between incubation and early chick-rearing periods for passive mobbing a 2 x 6 repeated ANOVA was performed. The first factor was Period (two levels: Incubation and Chick Rearing), the second factor was Time (six levels: Interval 1, Interval 2, Interval 3, Interval 4, Interval 5, Interval 6). Finally, a paired t-test was performed to test the difference in active mobbing behaviour between incubation and early chick-rearing. The dependent variable was the number of dives. All statistical analyses were performed using R statistical software.

Results

Differences in behaviour for single gulls between the two reproductive sub-periods, incubation and early chick-rearing. The repeated ANOVA showed significant differences for Period ($F_{1,22} = 25.67$, $P < 0.001$), for Behaviour ($F_{3,110} = 100.71$, $P < 0.001$) and for the Period x Behaviour interaction ($F_{3,66} = 28.06$, $P < 0.001$). Duncan Multiple Range Tests (DMRT) showed:

1) Significant differences for Flight (mean ± SD) from incubation (26.00 ± 4.63 seconds) to early chick rearing (18.33 ± 2.59 seconds; $p < 0.05$);
2) Significant differences between incubation (180.66 ± 17.51 seconds) and early chick-rearing for Landing (249.00 ± 32.52 seconds; $P < 0.05$);
3) Significant differences between incubation (196.00 ± 15.56 seconds) and early chick-rearing periods for Nest (309.17 ± 24.67 seconds; $P < 0.05$).

The comparison between incubation and early chick-rearing periods for Alert was not significant ($P > 0.05$).

Passive mobbing: The analysis showed statistically significant differences for Intervals 1, 2 and 3 both during incubation and early chick rearing. Each interval lasted 20 seconds, so the results must be attributed to the first minute of stay of the human intruder near the target nest. The repeated ANOVA showed significant results for Period ($F_{1,22}$ = 257.33, df = 5/10, P < 0.001), for Time ($F_{5,110}$ = 96.60, P < 0.001), and for the Period x Time interaction ($F_{5,110}$ = 122.96, df = 5/110, P < 0.001). DMRT showed:

1) Significant differences for Interval 1 from incubation (24.61 ± 4.68 mobbers) to early chick rearing (4.00 ± 2.58 mobbers; P < 0.05);
2) Significant differences for Interval 2 from incubation (23.61 ± 5.32 mobbers) to early chick rearing (2.78 ± 4.02 mobbers; P < 0.05);
3) Significant differences for Interval 3 from incubation (20.61 ± 7.17 mobbers) to early chick rearing (2.61 ± 4.50 mobbers; P < 0.05);
4) Differences for Interval 4, Interval 5 and Interval 6 were not significant (P > 0.05).

Active mobbing: The mean number of dives increases from 4.4 ± 2.1 to 11.2 ± 4.8 for incubation and chick rearing, respectively (t_{22} = 6.8, P < 0.01).

Discussion

Differences in behaviour for single gulls between the two reproductive sub-periods. The statistical analysis exhibits significant differences for the following behaviours: Flight, Landing and Nest. Gulls flew away more rapidly from the nest during chick rearing than during incubation when a human intruder approached. Moreover, the times of Landing and Nest were significantly longer during chick rearing than during incubation. This means that gulls went back to the nest more slowly during early chick rearing than during incubation. Likewise, during Alert, a trend to reduce the time of this behaviour during early chick rearing when compared to incubation was observed, but this result was statistically non-significant. This non-significant trend is probably due to a statistical 'floor effect': the alert times were so short that they do not allow for an effective discrimination.

In all likelihood, the differences are due to two factors. (1) The eggs are motionless, hence flying defence can be helpful but not crucial. As a consequence, the gulls tended to stay on the nest. In contrast, chicks can move and, in case of danger, it may be necessary to quickly move away from the nest. To do this, parents must fly away quickly and start a costly flying defence. In the end, the parents will come back to the nest only when all the chicks have come back to the nest, thereby explaining the longer times both for Landing and Nest.

The difference of intensity (energetic investment) of the nest defence behaviour can be attributed to the different value for the parents of an egg when compared to a chick (Montgomerie & Weatherhead 1988). Chicks represent more reproductive value than an egg and a strong increase of the nest defence behaviour in the early chick-rearing period has to be expected. Accordingly, the gulls flew away more rapidly during early chick rearing than during the incubation period. They immediately begin the attacks against the intruder and with alarm calls pushed the chicks to escape from the nest in search of rocks or other hiding places. In addition, gulls land and go back to their nests slowly. This behaviour is probably due to the fact that performing an attack from the sky against other gulls is more effective for birds than a ground attack. Subsequently, parents expect the chicks to return to the nest.

Importantly, our results confirm the hypothesis of behavioural modifications in single Yellow-legged Gulls in response to an approaching human intruder during the reproductive period (Jones *et al*. 2002). In this study the gulls modify the intensity of nest defence when a human intruder approached the nest in relation to the reproductive sub-period (i.e. chick rearing versus incubation), Furthermore, the intensity of nest defence increased during the chick-rearing period (e.g. Kruuk 1964; Horn 1968; Dill *et al*. 1999; Berzins *et al*. 2010).

Passive mobbing. In the current research it was decided to study active and passive mobbing separately. In fact, they have different adaptive goals and they are performed by different individuals (Shields 1984). Conover (1987) and later, Ostreiher (2003) have proposed an interpretation of the adaptive value of passive mobbing. The circular flight over the head of the disruptor aims to frighten and study the intruder in order to assess its level of danger as well as to study its strategy of attack. In addition, passive mobbing could have a more social purpose because it implies a collective action against the intruder. In contrast, active mobbing is more aggressive and aims to attack the intruders, driving them out from the disturbed nests. Moreover, active mobbing is usually performed by the parents of the disturbed nests. They emit mobbing calls and approach the intruder closely (less than 2 m) (Shields 1984) and perform dives against the intruder (Elliot 1984). In addition, passive mobbers are a random sample of a local population. They were silent and flew in circles at great distance (more than 3 m) from the stimulus (Shields 1984).

This part of the research aimed at verifying differences in size and intensity of passive mobbing by counting the maximum number of individuals in flight over the head of the human intruder during the two-minute stay nearby the target nest in the two distinctive reproductive sub-periods: incubation and early chick rearing. By dividing the data from these two reproductive periods into six separate sub-periods of 20 seconds each for a total two-minute observation time we aimed to study the changes in the size of mobbing over time. In this context, two changes were observed: a statistically significant reduction in the number of individuals taking part in the mobbing during the first minute of presence of the human intruder near the nest during the chick-rearing period; and a statistically non-significant reduction during the second minute of presence of the human intruder near the nest during the chick-rearing period. The latter observation can be interpreted as function of a reduction of passive mobbing over time (Kruuk 1976). This may have been due to the main purpose of passive mobbing: to gather information about the intruder. Once the gulls find out that the intruder is not dangerous, those coming from far away nests will go back first.

Concerning the difference in the size of passive mobbing during the reproductive sub-periods, data can be interpreted in the light of the social value of passive mobbing. In general, the intensity of nest defence increases after chicks hatch. In contrast, during incubation, a mainly altruistic behaviour was observed. As a matter of fact, most gulls exhibit a passive mobbing to help the gulls from the attacked nests. Conversely, during the early chick-rearing period, a more selfish behaviour was observed: every gull in the colony was focused on its own chick. Therefore, leaving their nest to help gulls or chicks from an attacked nest could be dangerous for their own progeny.

Active mobbing: This part of the research aimed at studying the differences in active mobbing during the two-minute stay of the human intruder near the target nest. Active mobbing is performed by the parents of the disturbed nests and consists in flying closely over the head of the disturber and performing dives. The average number of dives was chosen to highlight the intensity of active mobbing by the owners of the target nests. The average number of dives significantly increased during chick rearing when compared to incubation. Moreover, dives were performed nearer over the head of the human intruder and the legs of the gulls often hit the head of the disturber. Shields (1984) also observed that mobbing increased during the nesting period in comparison to incubation.

In conclusion, an efficient anti-predator behaviour is crucial for the survival of animals and risk-taking behaviours during the mating season increase reproductive success (Kruuk 1964; Horn 1968; Lima & Dill 1990). We observed that the nest defence behaviour increased during the breeding period for Yellow-legged Gulls at disturbed nests (i.e. selfish behaviour). In contrast, the size of passive mobbing (i.e. altruistic behaviour) decreased from chick rearing to incubation in agreement with Parental Investiment theory (Montgomerie & Weatherhead 1988).

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