2015

Ovulation Synchrony as an Adaptive Response to Egg Cannibalism in a Seabird Colony

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J. N. Andrews Honors Program
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HONS 497
Honors Thesis

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April 6, 2015

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Abstract

The predominant cause of egg loss in a large Glaucous-winged Gull (*Larus glaucescens*) colony in Washington is cannibalism. Previous work demonstrated the occurrence of every-other-day clutch initiation synchrony in dense areas of the colony during years when cannibalism was most frequent, suggesting that synchrony is an adaptive response to cannibalism. Here we show that (1) the initial egg laid in a nest is more likely to be cannibalized than subsequent eggs, (2) an egg is most likely to be cannibalized within the first 24 hours after it is laid, and (3) the odds that an initial egg is cannibalized within the first 24 hours decreases with an increase in the total number of initial eggs laid on that day. These findings support the hypothesis that clutch initiation synchrony functions as an adaptive response to cannibalism by increasing the odds that an initial egg will survive during its most vulnerable period.

Introduction

Every spring, breeding pairs of Glaucous-winged Gulls (*Larus glaucescens*) nest on Protection Island National Wildlife Refuge in the Strait of Juan de Fuca, Washington. Violet Point, a gravel spit on the east end of the island, contains a colony of approximately 1,500 nests. The colony contains multiple clubs – areas densely populated with nests – surrounded by regions of sparser net densities. From late May through June, female gulls lay three eggs at approximately 2-day intervals, designated in the order that they are laid as A, B and C eggs (Vermeer 1963).

Egg cannibalism, the predominant cause of egg loss in the Protection Island gull colony, increases with rises in sea surface temperature (SST); a 0.1 ^{0}C rise in SST is associated with a 10% rise in the odds that an egg is cannibalized (Hayward *et al.* 2014). Cannibalistic behavior occurs in over 1,300 species, ranging from lions to insects (Polis 1981). Although it can be influenced by a number of factors such as crowding, cannibalism is generally associated with low food availability (Fox 1975, Dong and Polis 1992). Increases in SST, for example during El Nino-Southern Oscillation (ENSO) events, decrease plankton concentrations at the base of the food web and lower ocean thermoclines; this forces surviving fish and other aquatic life to move to deeper water. As a consequence, Glaucous-winged Gulls, which cannot dive, have less food available and some resort to eating neighbors' eggs.

Henson *et al*. (2010) showed that every-other-day egg-laying synchrony can occur in clubs, with the degree of synchrony increasing with the density of nests in the club. This is analogous to menstrual synchrony among women living or working in close proximity (McClintock 1971). Given the two-day ovulation cycles of Glaucous-winged Gulls, egg-laying synchrony results in an every-other-day rise and fall in the number of eggs laid per day. Henson *et al*. (2010) also demonstrated that egg-laying synchrony was strongest at clutch initiation, meaning that gulls tended to lay their A eggs synchronously with other A eggs.

Henson *et al*. (2011) postulated that egg-laying synchrony is an adaptive response to egg cannibalism, suggesting that if more eggs are laid on the same day, each egg has a lower chance of being cannibalized. In particular, the observed strong clutch initiation synchrony might occur if (1) A eggs are cannibalized more heavily than B or C eggs, and (2) A eggs tend to be cannibalized within the first 24 hours after they are laid. Clutch initiation synchrony would be adaptive if the odds than an A egg is cannibalized within the first 24 hours is a decreasing function of the number of A eggs laid on that day.

In this study, I use data collected from the Protection Island gull colony from 2006–2011 to test the following null hypotheses:

1) A, B and C eggs are equally vulnerable to cannibalism within the first 24 hours after they are laid.
2) A eggs are cannibalized uniformly across time.
3) The losses of A eggs due to causes other than cannibalism exhibit the same temporal trends as losses due to cannibalism.
4) The odds that an A egg is cannibalized within 24 hours of being laid is unrelated to the number of A eggs laid on that day.

Methods

The Seabird Ecology Team monitored Glaucous-winged Gull nests and eggs in five rectangular sample plots centered on dense clubs on the Protection Island colony (48°07’40”n, 122°55’3”W), late May to early July, 2006–2011. A total of 1,432 nests and 3,398 eggs were monitored over the six-year period. Upon clutch initiation, each nest was staked and numbered, and thereafter checked for new eggs or egg loss each day. Each newly laid egg was marked as an A, B or C egg in the order that it was laid in the nest. Bald Eagle (*Haliaeetus leucocephalus*) predation and Glaucous-winged Gull egg cannibalism were the two primary sources of egg loss in the colony. Eagles tended to take all of the eggs in a clutch and eat them at the nest site, leaving behind fragments of eggshell, whereas cannibals typically stole only one egg from a nest which they would carry away, leaving behind no eggshell. For each egg lost during the laying season, investigators determined the cause of egg loss based on the presence or absence of eggshell fragments at the nest site (Hayward *et al.* 2014).

In the present study, I tallied the number of A, B and C eggs cannibalized within the first 24 hours after laying over the six year period. I used a 2x3 chi-squared test to compare numbers of A, B and C eggs cannibalized within the first 24-hour period, and I used a 2x2 chi-squared test to compare the number of A eggs cannibalized within the first 24-hour period with combined numbers of B and C eggs cannibalized within the first 24-hour period.

For each A egg lost to cannibalism, I recorded the number of days the egg survived after it was laid until it was lost. I then binned the A eggs lost to cannibalism over the six-year period by the number of days they survived after they were laid. I used a chi-squared test to compare the number of eggs lost after each interval to expected values calculated under the assumption that egg loss occurred uniformly over time. I performed the same procedure on A eggs lost to causes other than cannibalism. I repeated these procedures for the B and C eggs to determine if they exhibited egg loss trends similar to the A eggs.

Finally, for each day in which A-egg cannibalism occurred, I recorded the number of A eggs laid and the number of A eggs lost to cannibalism within the first 24 hours after laying. I used logistic regression in Matlab to test whether the odds that an A egg was lost to cannibalism within the first 24 hours after laying was related to of the number of A eggs laid that day.

Results

A eggs were cannibalized more heavily within the first 24-hour period than were B and C eggs. When I compared the cannibalism of A, B and C eggs within the first 24 hours after laying, I found that the B eggs were more vulnerable than the C eggs; moreover, the A eggs were more vulnerable than B and C eggs combined (Table 1).

Most cannibalism of A eggs occurred within the first 24 hours after laying, with the number of A eggs cannibalized dropping off each subsequent day during the first week. After the first week A egg loss was low and fluctuated only slightly from day to day (Fig 1A). Forms of A egg loss other than cannibalism did not exhibit significant loss within the first 24 hours after laying or any other observable trend (Fig.1B). Most cannibalism of B and C eggs occurred within the first 24 hours, but overall a smaller proportion of B and C eggs were taken than A eggs (Fig. 2).

Logistic regression demonstrated that, for days in which A-egg cannibalism occurred, the odds that an A egg was cannibalized within the first 24-hours after laying decreased 11% for each additional A egg laid on that day ($p<0.001$; OR=0.886).

Discussion

Although any egg in a clutch may be cannibalized at any point after it is laid, I demonstrated that A eggs were particularly vulnerable to cannibalism, especially within the first 24 hours after being laid. Because egg cannibals typically steal a single egg from unguarded nests, this vulnerability of A eggs is likely due to parental nest guarding habits (Hayward *et al.* 2014). When the first egg is laid in the nest, parent gulls spend less time guarding the nest, but become more protective with each new egg laid in the nest; once the clutch is complete, around-the-clock protection occurs as the parents begin to incubate the eggs (Vermeer 1963). A, B and C eggs all were particularly vulnerable to cannibalism within the first 24 hours after being laid, suggesting that eggs are not as carefully protected when they are first laid as they are in the days that follow. This vulnerability within the first 24-hour period was not exhibited in relation to other forms of egg loss, including eagle predation and loss due to flooding of nests by especially high tides. These forms of egg loss are largely unpreventable by the parent gulls guarding the nest.

We demonstrated that the odds an A egg is cannibalized within the first 24 hours decreased as the total number of A eggs laid that day increased. Because clutch initiation synchrony increases the total number of A eggs laid on a day, this synchrony confers an adaptive advantage by increasing an A egg's chance of survival during its most vulnerable period.

The role of clutch initiation synchrony as an adaptive response to egg cannibalism places reproductive synchrony in the larger context of climate change. Increases in sea surface temperatures lead to lower food supplies, causing gulls to resort to alternative forms of nutrition such as egg cannibalism (Hayward *et al.* 2014). In turn, egg-laying synchrony offers an adaptive advantage that allows gulls to minimize egg loss due to cannibalism. Short-term fluctuations in SST due to ENSO events or long-term rises in SST due to climate change can thus have a multi-faceted effect, influencing feeding strategies and, in turn, breeding strategies in Glaucous-winged Gulls.

The Salish Sea region of northwestern Washington has experienced a higher warming rate than the overall global warming trend, with SSTs increasing 1.0 ^{0}C from 1950–2005 (Snover *et al.* 2005). As this warming trend continues, egg cannibalism may pose a threat to the local gull population, which has been declining over the past decade (Cowles *et al.* 2012, Blight *et al.* 2015). Although we have shown that clutch initiation synchrony is adaptive in the presence of egg cannibalism, the long-term efficacy of this behavior in the face of long-term SST rise is unclear.

Acknowledgements

I thank Shandelle M. Henson, James L. Hayward, and WayAnne Watson for help with analysis and the 2006–2011 Seabird Ecology Team for help with data collection. I also thank the U.S. Fish and Wildlife Service for permission to work on Protection Island National Wildlife Refuge. This research was supported by U.S. National Science Foundation grants DMS 0314512 and DMS 0613899 to S.M. Henson and J. L. Hayward.

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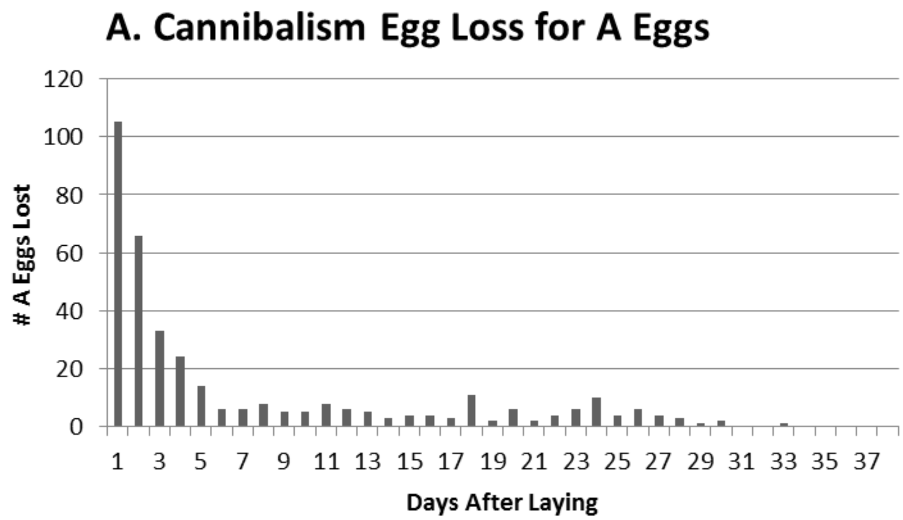
Table 1: A eggs were cannibalized more heavily within the first 24-hour period than B and C eggs and there was a significant difference in the number of losses to cannibalism among A, B and C eggs (χ^2=39.92, d.f.=2, $p<0.0001$). Moreover, there was a significant difference between the number of losses to cannibalism of A eggs and those of B and C eggs combined (χ^2=38.973, d.f.=1, $p<0.0001$).

	A Eggs	B Eggs	C Eggs
Cannibalized within 24 hours	105	40	20
Not cannibalized within 24 hours	1267	1154	812



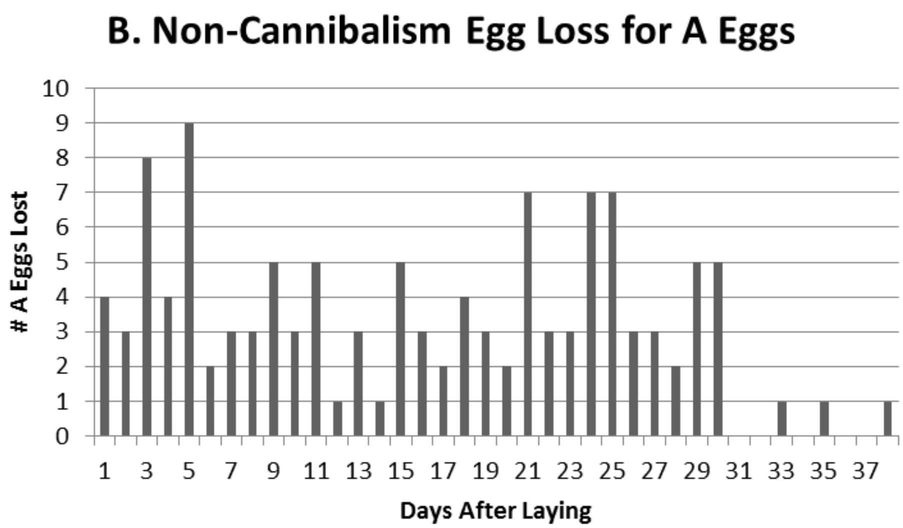


Figure 1: The number of A eggs lost to cannibalism and non-cannibalism events each day after laying, summed over the 2006–2011 breeding seasons. (A) Of the 367 eggs lost to cannibalism, 105 were lost within the first 24-hours after laying, with the number dropping off with each further day (χ^2 =966.7, d.f.=1, p<0.0001). (B) The distribution of cannibalism egg losses varied significantly from those for non-cannibalized eggs, which did not demonstrate a preponderance of egg loss during the first 24-hour period (χ^2=117.6, d.f.=37, p<0.001).

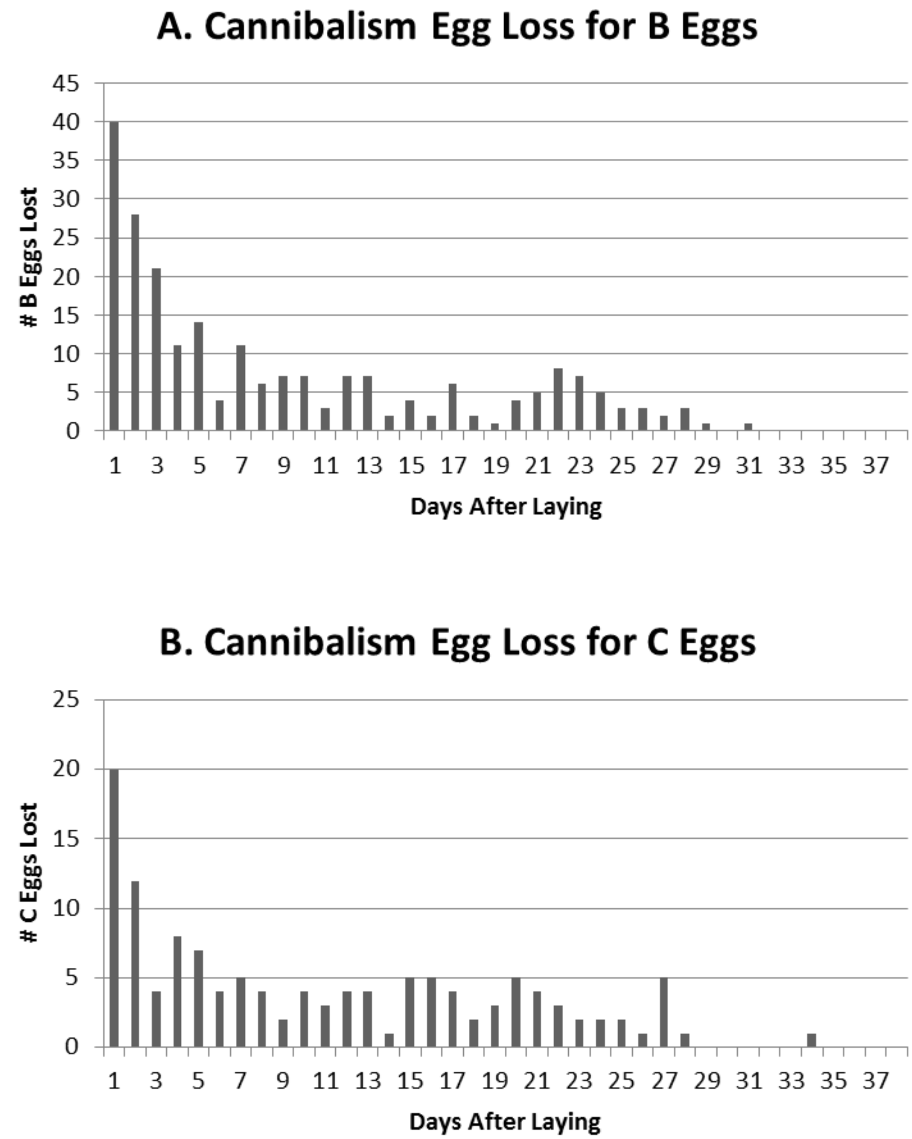


Figure 2: Cannibalism egg loss trends for B and C eggs over the 2006–2011 breeding season. The highest proportion of cannibalized B and C eggs were lost within the first 24 hours, although not at the levels exhibited for A eggs (B eggs: χ^2=197.08, d.f.=1, p<0.001; C eggs: χ^2=85.35, d.f.=1, p<0.001).