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Ashley A. Reichert

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The Behavior of Glaucous-winged Gull Egg Cannibals

Ashley A. Reichert
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Advisors: Dr. James L. Hayward and Dr. Shandelle M. Henson

Primary Advisor Signature:_________________
Secondary Advisor Signature:_________________

Departments: Department of Biology and Department of Mathematics
ABSTRACT—Cannibalism leads to a variety of behavioral, demographic, and ecological consequences and is influenced by a range of environmental circumstances among numerous taxa. Although multiple studies have linked cannibalism to egg and chick failure in gull populations, few characterizations of gull cannibal behavior and reproductive success exist. During the 2014 breeding season, we observed the territories of 16 Glaucous-winged Gull (Larus glaucescens) and Glaucous-winged × Western Gull (L. glaucescens × occidentalis) egg cannibal specialists on Protection Island, Washington, USA. We also monitored cannibal foraging behavior, relative reproductive success, and colony-wide egg loss. Cannibal specialists employed a variety of foraging and feeding behaviors and exhibited significantly lower reproductive success than non-cannibals. Future study of the Protection Island gull colony will monitor long-term trends in cannibalistic activity and behavior in relation to environmental change.

Keywords: Glaucous-winged Gull, Larus glaucescens, egg cannibalism, cannibal specialist, reproductive success, climate change
INTRODUCTION

Cannibalism, a process involving the predation and consumption of conspecifics, occurs widely throughout a variety of natural populations. Cannibalistic behavior has been reported for both carnivorous and otherwise herbivorous animals among diverse taxa, including planaria, protozoans, copepods, rotifers, gastropods, insects, fish, birds, and mammals (Fox 1975, Polis 1981); Polis (1981) noted that cannibalism accounts for a major source of mortality in close to 1,300 species. In addition to shaping social behaviors within a population, intraspecific predation may influence a host of demographic and ecological circumstances, including population size, age distribution, population density, and reproductive success (Fox 1975, Polis 1981, Hayward et al. 2014).

Numerous studies have linked cannibalism to extensive egg and chick failure in bird species; cannibalism accounted for nearly 25% of chick deaths in a population of Herring Gulls (Larus argentatus; Parsons 1971) and large proportions of egg or chick loss in Ring-billed Gulls (L. delawarensis; Brown and Lang 1996), crows (Corvus corone; Polis 1981), and Glaucous-winged Gulls (L. glaucescens; Hayward et al. 2014). Possible circumstances augmenting the presence and intensity of cannibalism in bird populations include depressed food supplies (Paullin 1987, Boal and Bacorn 1994) and unseasonable or prolonged trends in temperature (Paullin 1987, Hayward et al. 2014). For example, a recent six-year study of Glaucous-winged Gulls and Glaucous-winged × Western Gull (L. glaucescens × occidentalis) hybrids at Protection Island National Wildlife Refuge, Washington, USA, demonstrated that increased egg cannibalism results from rises in local sea surface temperature (SST) and concurrent decreased food supply (Hayward et al. 2014).

Although cannibalism is a commonly observed phenomenon in gull populations (e.g.,
Parsons 1971, Brown and Lang 1996, Hayward et al. 2014), few descriptions of the behaviors and life history characteristics of egg cannibal specialists—gulls that feed predominantly on conspecific eggs—exist. This study involves a characterization of the behaviors, locations, and hatching success of cannibal specialists within the Violet Point Glaucous-winged Gull and Glaucous-winged × Western Gull (L. glaucescens × occidentalis) colony on Protection Island during the breeding season of May–June 2014. Building upon the findings of Hayward et al. (2014), we tested the predictions that 1) male gulls cannibalize eggs more frequently than females, 2) the amounts of egg cannibalism remain constant throughout the breeding season, 3) egg cannibalism occurs more frequently in the early morning and late evening, and 4) egg cannibal specialists exhibit greater hatching success and larger clutch sizes than non-egg cannibals.

**METHODOLOGY**

**Study Site and Egg-laying Data**

This study took place on Protection Island National Wildlife Refuge (48°07′40″N, 122°55′3″W), Jefferson County, Washington, USA, located at the east end of the Strait of Juan de Fuca. The island’s southeastern gravel spit, Violet Point, sustains a breeding colony of over 1,500 pairs of Glaucous-winged Gulls and Glaucous-winged × Western Gull hybrids (Moncrieff et al. 2013).

To monitor seasonal trends in egg laying, five rectangular study plots of various dimensions were selected (Fig. 1). The plots contained a combined total of 273 nests and covered a range of nesting habitats within the more densely nested areas of the colony. From late May to mid-July, each nest within the plots was examined daily in the late afternoon and marked with a
numbered, wooden stake upon clutch initiation. Eggs were marked in order of laying (A, B, C, etc.) using permanent marker, and any occurrence of egg loss or hatching was noted. The plots provided a representative sample of the various habitats utilized by gulls in the Violet Point colony.

**Identification of Cannibal Territories**

The most prevalent sources of gull egg predation on Protection Island include Bald Eagles (*Haliaeetus leucocephalus*) and cannibalistic gulls; Bald Eagles often destroy entire nests and may even injure or kill the accompanying adult gulls, whereas cannibals tend to remove single eggs from unguarded nests and fly back to their own territories before devouring the eggs (Hayward et al. 2014). Thus, territories of egg cannibal specialists are often littered with fragmented eggshell.

To identify the territories of such specialists, we carried out colony-wide searches on an every-other-day basis—examining half the colony on one day and the other half on the following day. We began the searches at the first evidence of egg loss (1 June) and repeated this schedule until multiple hatchings occurred (30 June). Any area found to contain eggshell fragments was marked with numbered, wooden stakes and monitored on a daily basis for the remainder of the study. If regular accumulation of eggshell occurred at a previously marked area, we recorded that location as a cannibal territory and monitored egg laying within the territory in addition to accumulations of broken eggshell. A Trimble GPS and ArcGIS Desktop 10 (2011) were used to record and map the positions of each predated egg and cannibal territory to within 10 cm accuracy.
Eggshell and Pellet Collection

Fragmented eggshells within cannibal territories were collected daily at 3-hr intervals, with the first collection time beginning at 0600 and the final collection time at 2100. After allowing the eggshells to completely dry, we measured eggshell masses from each collection interval and cannibal territory. The recorded eggshell masses and the average mass of an intact eggshell were used to approximate 1) the consumption of eggs per territory at a given time interval, 2) the daily consumption of eggs per territory, and 3) the seasonal trend in egg consumption. In addition to mass measurements, we examined the fracture patterns of collected eggshells to further characterize the modes of cannibalistic egg consumption.

At each 3-hr interval, we also collected any regurgitated pellets found within cannibal territories. Because pellets contain the undigested components of a bird’s food, visual analysis of the pellets provided a simple method to determine specific diets of individual gulls (Vermeer 1982). Pellets removed from the territories of cannibal specialists were compared to pellets of non-cannibal gulls, and any differences in pellet composition or appearance were noted.

Observation of Individual Cannibal Specialists

To characterize specific feeding and behavioral patterns of egg cannibals, we designated five particularly active cannibal territories for observation. Each territory was visually monitored, either intermittently from an observation blind erected within the colony or by using a Sony Handycam HDR-SR12 to record events in the territories for 2- to 3-day periods. Specifically, we used such observations to determine 1) the foraging behaviors of egg cannibal specialists, 2) the sex of active egg cannibals, 3) the situational and environmental contexts during which egg cannibalism most commonly occurred, and 4) the methods used by gull
cannibals to puncture and consume stolen eggs.

Comparison of Reproductive Success

On 24 June 2014, we obtained mean clutch sizes for three groups: 1) known egg cannibal specialists, 2) gulls nesting in immediate proximity to cannibal territories (to serve as a control), and 3) gulls nesting within the five study plots. For the egg cannibal group, the mean clutch size was determined based on the number of eggs laid in nests belonging to cannibal pairs. However, if the location of a cannibal pair’s nest was uncertain, we used the average clutch size of the three closest nests for that particular territory. For the control group, we used a random number table to generate a list of random compass readings; from each cannibal territory, we walked 15 paces in the direction of a particular compass reading and then averaged the clutch sizes of the five nearest nests. This group represented gulls nesting in the same habitat conditions as the cannibal pairs. Under the assumption that larger clutch sizes represent greater reproductive success, we compared the mean clutch sizes of each of the three groups as a measure of relative reproductive success.

Statistical Analyses

To determine the times of day eggs were most often cannibalized, a one-way analysis of variance (ANOVA) was used to compare masses of eggshell fragments collected at each of the six daily collection times. If a significant difference ($p < 0.05$) in eggshell mass was found among the six collection times for a given territory, a Bonferroni correction pairwise comparison test was used to test for differences between pairs of collection times.

To examine relative reproductive success, we compared each of the three mean clutch
sizes using a Mann-Whitney U test, which identified any significant differences between mean clutch sizes. A significantly lower (p < 0.05) average clutch size was considered to represent relatively poor reproductive success.

RESULTS

Locations of Cannibal Territories

A total of 16 cannibal territories were identified; five of these 16 pairs were “super cannibals,” feeding almost exclusively on cannibalized eggs. Most of the cannibal territories were located in sparse, peripheral areas of the colony, whereas territories within the five study plots were in locations of more central, dense nesting (Fig. 2).

Seasonal Egg Laying and Cannibalism

Colony-wide cannibalistic activity occurred with egg laying, primarily between 1 June and 30 June; the highest frequency of both egg laying and cannibalism occurred around 9–10 June (Fig. 3). We thus observed less cannibalism at the beginning and end of the breeding season than in the middle. Daily eggshell mass totals from the 16 cannibal territories were significantly correlated with daily laying of new A eggs (R = 0.66, df = 27, p = 9.83 × 10⁻⁵; Fig. 4A), new B eggs (R = 0.72, df = 27, p = 1.16 × 10⁻⁵; Fig. 4B), and new C eggs (R = 0.73, df = 27, p = 7.54 × 10⁻⁶; Fig. 4C) in the five study plots.

Eggshell Breakage Patterns and Pellet Composition

For a total of 302 cannibalized eggs, the four most common breakage patterns included pecking (12.9%), biting (17.9%), halving (23.2%), and fragmenting (33.8%), with the remaining
eggs not falling into any of these categories (Fig. 5). Although fragmenting of the eggs seemed most common among the 16 territories, this trend varied depending on individual cannibal pairs; for example, in a particular super cannibal territory, 64.1% of the eggs collected were either bitten or halved, whereas only 7.8% were fragmented.

Nearly all the pellets collected from cannibal territories contained fragments of eggshell, whereas non-cannibal pellets contained a variety of non-eggshell components, including fragmented crab exoskeleton and plant debris (Fig. 6A–D).

**Egg Cannibal Foraging Behaviors**

Two cannibalistic foraging tactics were observed between 1 June and 30 June: the “disturbance tactic” and the “flight tactic.” Gulls employing the disturbance tactic took advantage of colony disturbances, created usually by Bald Eagles and occasionally by humans, to remove eggs from unprotected nests. Gulls that did not regularly cannibalize were also occasionally observed stealing eggs during opportunistic disturbances, although most of this activity was carried out by known cannibal specialists. The less common foraging behavior, the flight tactic, involved cannibal specialists flying slowly above the colony during undisturbed times, looking down while flying, and diving to retrieve eggs from poorly guarded nests. The flying bouts lasted anywhere between 4 min to over an hour.

Egg cannibal specialists obtained eggs at different times of day depending on the particular foraging pattern employed. For three of the four super cannibals that used the disturbance tactic (Fig. 7A–C), significantly more eggshells were collected at the 0600 collection time than at any other time of day ($F_{5, 90} = 7.7662, p < 0.0001$; $F_{5, 90} = 12.4689, p < 0.0001$; $F_{5, 90} = 2.4745, p = 0.0379$, respectively). However, the two super cannibals that usually employed the
flight tactic (Fig. 7D–E) showed no significant difference in the amounts of eggshell collected at the six collection times ($F_{5, 90} = 1.3157, p = 0.2646; F_{5, 90} = 2.1301, p = 0.0689$, respectively).

**Behavioral Trends in Egg Cannibal Specialists**

Patterns in cannibalistic behavior were determined from over 200 hr of video footage of the five super cannibal territories; videos contained 43 visible cannibalism events.

Preceding a typical cannibalism event, a male gull left his territory while the female mate remained; the male’s departure often followed a disturbance or food-begging behavior (Tinbergen 1953) by the female, or with no apparent antecedent behavior. Upon his return, the male held the stolen egg in his beak, and the female often immediately head-tossed (Tinbergen 1953) at the sight of the male. The male then punctured the egg with his beak, and either the male or both members of the pair ate the contents of the egg. If both members of the pair consumed the egg, the female often took occasional breaks from eating to head-toss while the male continued pecking at the egg. When allowed by the male, the female ate for approximately 1–3 min (compared to 5–8 min for the male). In seven of the recorded cannibalism events, however, the male actively prevented the female from eating, either by biting and pecking the female, moving the egg to another location within the territory, or swallowing the egg when the female approached.

One cannibal territory revealed fairly atypical cannibalistic behavior. In 10 out of the 12 observed cannibalism events in this territory, the male gull returned to the territory with an egg held completely in his crop. Usually, this male then regurgitated the egg and ate alone while the female remained on the nest. The two times an egg was brought back intact in the male’s beak (rather than in his crop), he immediately swallowed the egg whole when the female approached.
The male never actively shared the cannibalized eggs with his mate during the observation periods.

**Comparison of Reproductive Success**

Mean clutch sizes for cannibal territories, control territories, and territories within the five study plots on 24 June 2014 were 0.60, 0.85, and 2.09, respectively. Mann-Whitney U analysis showed that cannibal territories had significantly smaller clutch sizes than both control territories (p = 0.0138) and study plot territories (p = 8.63 × 10^-30).

**Cannibalism Totals and Rates**

Throughout the 2014 breeding season, 16 cannibal specialists ate approximately 250 eggs between 1 June and 30 June; two super cannibals brought in more than 80 eggs each during this same period. From the daily colony-wide scans, a total of at least 270 broken eggshells not associated with known cannibal territories and not from hatched eggs were also found. Assuming most of these broken eggshells were associated with cannibalism rather than Bald Eagle predation, approximately 500 eggs were likely cannibalized between 1 June and 30 June.

A total of 1,546 nests were counted in a complete survey of the colony. Given that the final average clutch size (through 15 July) for the five study plots was 2.48, total egg production for the 2014 season was estimated to be 3,840 eggs. Therefore an estimate of 500 cannibalized eggs suggests an approximate colony-wide cannibalism rate of 13.0%. However, this estimate includes data only from the month of June. Because cannibalism continued into mid-July, the true rate is likely considerably higher. From nests in the five study plots, 249 out of 1158 total laid eggs were cannibalized throughout the entire season, yielding a cannibalism rate of 21.5%
within the study plots alone. This is likely a more representative estimate of colony-wide cannibalism because this value includes data from both June and July.

**DISCUSSION**

Throughout the study, nest locations of egg cannibal specialists were consistently found in low-density, peripheral areas of the colony and were characterized by poor reproductive success relative to more central nesting areas (such as the five study plots). Previous studies have suggested that nest location and density heavily influence breeding success in colonial birds. For example, decreased clutch size, hatching rates, and chick survival were characteristic of Herring Gulls (Parsons 1976), Ring-billed Gulls (Dexheimer and Southern 1974), Adelie Penguins (*Pygoscelis adeliae*; Tenaza 1971), Black-legged Kittiwakes (*Rissa tridactyla*; Aebischer and Coulson 1990), and Black-headed Gulls (*L. ridibundus*; Patterson 1965) that nested at lower-than-normal densities or in colony fringes. Although the reason for cannibals nesting in areas of low productivity remains unknown, Parsons’ (1971) findings provide a potential explanation: Herring Gull cannibals preyed on nests in significantly lower-density areas of the colony. If the gulls we observed similarly cannibalize nests located in less dense, peripheral areas of the colony, perhaps there exists an advantage to nesting nearby their sources of food. However, a more thorough, colony-wide study of predated nests is necessary to address this hypothesis.

The significant correlation between cannibalized eggs and newly laid eggs—including the peak in cannibalism at the height of egg laying—falsified our prediction of constant seasonal amounts of cannibalism (which Parsons [1971] initially observed in Herring Gulls). In addition, this finding suggests that perhaps newly laid eggs are more vulnerable to cannibalism than “older” eggs, since the prevalence of cannibalism seemed dependent on the availability of new
eggs. A number of ecological cues may account for this observation. For instance, the increase in cannibalism during peak egg laying was due not only to higher amounts of cannibalism per individual but also to an increased number of gulls participating in cannibalistic activity. Because gulls are adaptable, opportunistic feeders (Vermeer 1982, Barry and Barry 1990), perhaps individuals that normally avoided cannibalism took advantage of the growing availability of new eggs during mid-season and contributed to the observed spike in cannibalistic activity. The peak in cannibalism may also be related to the physiological needs of breeding gulls. Blight (2011) described Glaucous-winged Gulls as having high energetic and nutritional costs of egg production and laying. If other food sources were insufficient to meet the nutritional constraints required by egg production, perhaps additional, normally non-cannibalistic gulls turned to egg cannibalism as a supplementary source of food during the height of egg laying.

Regardless of the cannibal territory, the four egg fracture patterns—pecking, biting, halving, and especially fragmenting—were frequently observed throughout June. Although the patterns are not sufficient to distinguish between individual cannibals alone, they may be useful for distinguishing cannibalized eggs from eagle-predated eggs. In over six weeks on the Violet Point colony, we rarely saw an egg fragmented or halved from a Bald Eagle attack; rather, eagles often left predated eggs with either deep slashes diagonal to the egg axis or with wide, jagged openings on one side of the egg. The ability to reliably differentiate eagle-predated and cannibalized eggs could optimize future estimations of colony-wide egg cannibalism.

Out of all the pellets collected from cannibal territories between 1 June and 30 June, nearly every pellet contained various sizes of fragmented eggshell. Given that these eggshell fragments were not included in the weighing of collected eggshells from the 16 cannibal territories, the eggshell masses we recorded are likely poor representations of the true numbers of
eggs that were cannibalized. The multiple observations of gulls swallowing cannibalized eggs likewise suggest the possibility of underestimating cannibalism rates when eggshell mass is the sole consideration. Future attempts to quantify cannibalistic activity using mass measurements should certainly take this underestimation into account.

Nearly all egg cannibal specialists utilized the disturbance tactic—cannibalizing eggs during times of relative chaos—and only two gulls were observed employing a specific flight tactic to forage for eggs. Neither foraging behavior strongly conferred reproductive benefit (as evidenced by the significantly lower average clutch size of egg cannibals); on the contrary, both behaviors seemed to share the possibility of disadvantageously influencing survival and reproduction. Males using the flight tactic, for example, were often absent from their territory for hours at a time. Norberg (1977) describes the energy expense of locomotion as a major physiological cost in birds participating in foraging activities. Beyond individual energetic tolls of long foraging bouts, the low territory attendance of the males may jeopardize the survival and success of any offspring remaining within the territory (Hunt Jr. 1972, Bukacińska et al. 1996). The disturbance tactic, too, may pose potential threats to cannibal specialists. Whereas typical gull behavior during a Bald Eagle attack includes nearby gulls flying into the air to attack or avoid the eagle (Hayward et al. 1977, 2010, Galusha and Hayward 2002), some cannibal specialists were observed flying toward distant eagle disturbances—putting their lives in danger even when their own territories were not at risk—in order to cannibalize unguarded eggs. Whether these behaviors endanger cannibal specialists more or less than the foraging tactics of non-cannibal gulls remains unknown.

The finding that gulls that utilize the disturbance tactic cannibalize more frequently between 2100 and 0600 resembles the observations of Atkins et al. (in preparation), who showed
that egg loss due to cannibalism occurred more frequently in the early morning than any other time of day. Because cannibalism events often occur during eagle disturbances, the frequent cannibalism activity in the early morning could serve as a fairly reliable indicator of concurrent early morning Bald Eagle activity. Conversely, the few gulls that utilized the flight tactic showed no particular pattern in timing of cannibalism events, likely because these gulls were far less dependent on colony disturbances than were other cannibal specialists. Although Galusha and Hayward (2002) reported an increase in total Bald Eagle flight activity between 0600 and 1400 in the late breeding season (July–August), our findings could suggest an increased late-evening and early-morning (2100–0600) activity of eagles at the height of the laying season (June).

Regardless of the foraging tactic, the 16 observed cannibal territories displayed unexpectedly lower reproductive success than any other observed area of the colony. Fox (1975) and Polis (1981) described cannibals as often having direct nutritional and energetic benefits when other food sources were lacking, which led to the aforementioned prediction that cannibal specialists would have greater relative reproductive success than non-cannibal gulls. Although the specific cause of the low clutch size observed among cannibals is uncertain and likely depends on a wide variety of ecological and social circumstances, there are two possible explanations that could benefit from further investigation: First, the cannibal specialists may undergo a tradeoff between offspring production and increased nourishment in times of food scarcity; Reid (1987), for example, described a decreased survival of breeding Glaucous-winged Gull adults due to the physiological expense of reproduction. Perhaps the cannibals we observed experience a greater potential for future reproduction when they allocate more energy to feeding than to reproducing during seasons of decreased food supply. A second explanation for the lower reproductive success of cannibal pairs could be related to the multiple observed instances of
cannibalistic gulls actively refusing to share cannibalized eggs with their female mates.

Normally, courtship feeding serves as an important source of the female’s nutrition in days leading to and during egg laying (Salzer and Larkin 1990). If cannibalistic males exercise little or no courtship feeding during the breeding season, this could place a constraint on the reproductive capability of the female.

Starvation and lack of food are among the most prominent ecological circumstances associated with cannibalism (Dong and Polis 1992). Hayward et al. (2014) attributed food shortages in the Violet Point gull colony to prolonged rises in sea surface temperature (SST)—especially during El Niño-Southern Oscillation (ENSO) events—which drive down ocean thermoclines, weaken upwellings, and send remaining forage fish to deeper water. The ensuing decreased productivity of surface waters poses a threat to non-diving seabirds, such as gulls, that depend on fish for survival. If SST in the Strait of Juan de Fuca continues to rise in response to climate change, increasing levels of cannibalism could lead to population declines for Glaucous-winged Gulls. Further study will involve monitoring climate change in relation to the frequency and occurrence of egg cannibalism, as well as the behavioral qualities and trends of egg cannibal specialists.

LITERATURE CITED


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FIGURE CAPTIONS

Figure 1. Aerial view of the Protection Island gull colony on Violet Point. White lines indicate the boundaries of five study plots, in which egg laying and egg loss were monitored daily during the 2014 breeding season.

Figure 2. Aerial view of the Protection Island gull colony. Red circles represent the territories of egg cannibal specialists, yellow squares represent locations of observational cameras, and black circles represent areas outside of cannibal territories where broken eggshells were found.

Figure 3. Comparison of the number of cannibalized eggs and the number of new eggs laid per day throughout June 2014. Cannibalistic activity peaked with the peak laying of A eggs (the first egg of a clutch).

Figure 4A–C. Comparisons of daily eggshell mass totals and the number of new eggs laid. Cannibalized eggshell masses were positively correlated with new A eggs (A), new B eggs (B), and new C eggs (C).

Figure 5A–D. Common breakage patterns of cannibalized eggs. Eggshells found in cannibal territories were usually either pecked (A), bitten (B), halved (C), or fragmented (D).

Figure 6A–D. Examples of pellets collected from cannibal and non-cannibal territories. Pellets of cannibal specialists contained fragments of eggshell (A, B), whereas non-cannibal pellets contained other materials—including crab exoskeleton (C) and plant debris (D).

Figure 7A–E. Total eggshell masses found in super cannibal territories during the 2014 breeding season. Eggs were cannibalized at different times of day depending on the particular foraging tactic used by the cannibal. The cannibals employing the disturbance tactic cannibalized significantly more frequently between 2100 and 0600 (A, B, C), whereas cannibals employing the flight tactic showed no particular trend in the timing of cannibalism (D, E).
Figure 1
Figure 2
Figure 3
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Figure 5
Figure 6
Figure 7