INTRODUCTION

In North America, Glaucous-winged Gulls *Larus glaucescens* breed in dense colonies along the Pacific and Bering Sea coasts, from northwestern Oregon to western Alaska (Hayward & Verbeek 2008, BirdLife International 2019). Like other ground-nesting gulls, Glaucous-winged Gulls are indeterminate egg layers (Parsons 1976), meaning that when eggs are depredated or taken from the nest during the period when clutches are being completed, the female continues to lay replacement eggs until the clutch is complete (three eggs on average; Hayward & Verbeek 2008). If the clutch is lost during incubation (typically 27 d; Hayward & Verbeek 2008), the female must wait 12–13 d for follicle development before laying a replacement clutch (Vermeer 1963, Verbeek 1986).

In Alaska, there is a long tradition of harvesting Glaucous-winged Gull eggs for subsistence purposes, although the collection of migratory bird eggs without permit became illegal after the passage of the Migratory Bird Treaty Act in 1918. Legal mechanisms allowing for subsistence egg takes began on a regional basis in 2003 (USFWS 2002). Beginning in 2014 on the Copper River Delta in southcentral Alaska, gull eggs could be legally harvested for subsistence purposes from 01–31 May by all residents of the nearby town of Cordova and two small villages of Prince William Sound (Fig. 1; USFWS 2014).

Previous studies have documented reduced hatch success and colony failures within gull colonies after human disturbance and egg collection activities (Hunt 1972, Robert & Ralph 1975, Vermeer et al. 1991). In contrast, other studies indicate that infrequent harvests early in the breeding season can limit the impact on the hatch success of gulls (Zador 2001, Zador et al. 2006, Zador & Piatt 2007). To resolve this inconsistency, we examined the effects of experimental egg removal on the egg laying patterns of Glaucous-winged Gulls nesting in a colony that was recently made accessible for legal subsistence harvest in southcentral Alaska (Fig. 1).

STUDY AREA AND METHODS

This experiment took place 14 May–12 June 2018 in a large Glaucous-winged Gull colony (10000 individuals; North Pacific Seabird Data Portal 2018) on Egg Island (60.39°N, 145.98°W), a barrier island on the western edge of the Copper River Delta in southcentral Alaska (Fig. 1). Egg Island is uninhabited by humans and hosts the second highest population of Glaucous-winged Gulls in the Gulf of Alaska after nearby Middleton Island (North Pacific Seabird Data Portal 2018). We conducted our study in a subcolony on the southwestern tip of the island, an area that is visited infrequently by locals, reducing the confounding effects of disturbance unrelated to our study.

We established two treatment plots of approximately the same size in non-contiguous areas of the gull subcolony. In Plot A, we...
removed one egg from each of 20 randomly selected nests having incomplete clutches (< 3 eggs) during the laying period to mimic traditional harvest practices. Eggs were removed from 10 one-egg nests and 10 two-egg nests. We then floated the eggs to estimate incubation stage following Schreiber (1970). Each nest was marked using GPS, and a small, flagged stake was placed 2–3 m away. We labeled eggs not selected for removal with a felt-tipped marker. In Plot A, our control, we monitored 12 randomly selected one-egg nests and eight two-egg nests. At the time of plot delineation there were only eight nests containing two eggs, hence the unbalanced sample size. Nests were marked and eggs labeled, but no eggs were removed. In both plots, we monitored nests twice during egg-laying (14 May, 15 May) and four times during incubation (23 May, 24 May, 03 June, 12 June). We noted any potential nest predators observed in the area and documented instances of nest predation following Anthony et al. (2004).

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We used R version 2.12.1 (R Development Core Team 2010) to perform Mann-Whitney-Wilcoxon tests (Mann & Whitney 1947) to determine if differences in the mean total number of eggs laid per nest and mean final clutch size were statistically significant ($P \leq 0.05$) between study plots. Averages are reported with standard error unless otherwise specified.

RESULTS

Nest manipulation

Based on egg flotation patterns and the number of eggs in the nest, eggs were removed from the one- and two-egg nests within an estimated two and four days of laying, respectively. Within 24 h of egg removal, 35% ($n = 7$) of the nests were abandoned and remained empty for the duration of the study. All abandoned nests were one-egg nests that became empty nests upon manipulation. Pairs continued to lay, on average, 0.80 ± 0.21 eggs after egg removal. Gull pairs in Plot A laid, on average, 2.30 ± 0.24 eggs in total and achieved a mean final clutch size of 1.30 ± 0.24 eggs (Table 1, Fig. 2). In all, only two of 20 monitored nests (10%) in Plot A achieved a complete clutch of three eggs by laying a fourth egg. Both were one-egg nests at the time of egg removal.

In Plot B, most pairs (85%) continued to lay eggs after our initial visit, with 15 nests (75%) achieving a complete clutch. Two nests were abandoned within the 24-h period following our initial visit and remained empty for the duration of the study. Pairs laid, on average, 2.75 ± 0.16 eggs in total and achieved a mean final clutch size of 2.65 ± 0.15 eggs (Table 1, Fig. 2). We found no significant differences in the total number of eggs laid per nest across plots ($P = 0.18$). However, the final clutch size in Plot B was significantly larger than the final clutch size in Plot A ($P = 0.000053$; Fig. 2).

Natural predation

Over the course of the study, no eggs from monitored nests in Plot A were lost to predation or other natural causes. In Plot B, we documented five instances of egg loss from monitored nests. In the 24-h period between nest visits on 14 May and 15 May, four nests lost an egg (three one-egg nests and one two-egg nest). No shells or egg remnants were observed in or around nests. The gull pair from the depredated two-egg nest laid one more egg and achieved a final clutch size of two eggs. Two of the one-egg nests were abandoned after predation and remained empty for the remainder of the study. The other depredated one-egg nest subsequently achieved a full clutch of three eggs by 23 May but had lost another egg by the time we visited the nest again on 03 June. No shell fragments were found in the nest, but a bloody half-shell was found ~ 4 m away.

DISCUSSION

Nest manipulation

Given that Larus gulls are reported to lay eggs indeterminately (Parsons 1976), we expected gull pairs in the manipulated plot to lay more eggs to compensate for the loss of an egg during the laying phase. Instead, we found no difference in the total number of eggs laid per nest across study plots. Glaucous-winged Gull pairs in the manipulated plot had significantly smaller final clutch sizes

| Table 1 | Comparison of the Glaucous-winged Gull nest manipulation experiment results across the manipulated (Plot A) and non-manipulated (Plot B) study plots on Egg Island, Alaska, May–June 2018 |
|-----------------------------|-----------------------------|-----------------------------|
|                             | Plot A                      | Plot B                      |
|                             | (1-egg nests/ 2-egg nests)  | (1-egg nests/ 2-egg nests)  |
| Number eggs removed         | 10/10                       | 0/0                         |
| Number nests immediately abandoned | 7/0                        | 2/0                         |
| Number depredated eggs      | 0/0                         | 4/1                         |
| Number depredated nests     | 0/0                         | 3/1                         |
| Proportion of nests achieving complete clutch | 0.20/0.00 | 0.67/0.88 |
| Total number eggs laid      | 46a                        | 55                          |
| Mean number eggs per nest   | 2.30 (± 0.24)               | 2.75 (± 0.16)               |
| Mean final clutch size      | 1.30 (± 0.24)               | 2.65 (± 0.15)               |

* Includes experimentally removed eggs
compared with the non-manipulated plot, with mean clutch size in the non-manipulated plot more than double that of the manipulated plot. In fact, only two nests in the manipulated plot achieved a complete clutch of three eggs, compared with 15 nests in the non-manipulated plot.

After egg removal, seven manipulated one-egg nests were immediately abandoned. Unfortunately, we were unable to track whether gulls that had abandoned their nests after manipulation continued laying in another nest within their territory, as has been documented at other sites (Washington: Reid 1988; Alaska: Zador 2001). However, no pairs having a two-egg nest in the manipulated plot completed a full clutch after egg removal by laying a fourth egg, indicating that the gulls in this study did not compensate for eggs that were experimentally removed from their nests.

In contrast, at a colony in southeastern Alaska, Glaucous-winged Gulls completed a clutch of three by laying a fourth egg in 78% of nests after their first egg was experimentally removed immediately after laying (Zador 2001). Furthermore, pairs with their first egg removed laid 1.24 and 1.06 more eggs (in the first and second year of the study, respectively) than gulls in the non-manipulated group. Similarly, Parsons (1976) reported that Herring Gulls L. argentatus with first eggs removed laid a fourth egg in 59% of nests.

Forage availability is a limiting factor of seabird reproductive success (Cairns 1988, Suryan et al. 2002), including that of west coast Western Gulls L. occidentalis (Ainley & Boekelheide 1990) and Glaucous-winged gulls (Murphy et al. 1984, Bliht 2011). Egg production is energetically costly for gulls (Houston et al. 1983), which are capital breeders, meaning females obtain the resources for egg production prior to the breeding season. Therefore, the inability of gulls to compensate for removed eggs in this study may be related to limited forage availability.

Immediately prior to the breeding season, gulls congregate in the town of Cordova to feed on fish offal discharged from local fish processing plants. Once nesting commences, breeding gulls leave town and remain near their colonies on barrier islands of the Copper River Delta (MAB unpubl. data). These barrier islands border the North Pacific Ocean, a region which recently experienced a dramatic multi-year marine heatwave during 2014–2016 (Bond et al. 2015, Di Lorenzo & Mantua 2016). The persistently warm water mass altered food web dynamics and coincided with seabird colony failures across the Gulf of Alaska (Dragoo et al. 2017, 2018; Zador & Yasumiishi 2018), including the Egg Island Glaucous-winged Gull colony (MAB unpubl. data) and a nearby Caspian Tern Hydroprogne caspia colony (Suzuki et al. 2019). Although the heatwave had moderated by the 2018 breeding season, sea surface temperatures remained above the long-term mean (Zador & Yasumiishi 2018). The reduced clutch sizes of Glaucous-winged Gulls in our study, as well as the low reproductive success of surface-feeding Black-legged Kittiwakes Rissa tridactyla on nearby Middleton Island (~ 100 km south) in 2018, suggested that marine food web dynamics had not yet recovered (Institute for Seabird Research and Conservation 2018).

Natural predation

Although several potential predators are present on Egg Island (e.g., the Common Raven Corvus corax, Short-eared Owl Asio flammeus, and Northern Harrier Circus hudsonius), Bald Eagles Haliaeetus leucocephalus and cannibalistic adult Glaucous-winged Gulls appeared to be the main predators of gull eggs in our study, a finding that is similar to other study sites in North America (Zador 2001, Cowles et al. 2012, Hayward et al. 2014). Egg loss to depredation was minimal for the nests in our study, with only five instances of egg loss from four of 40 monitored nests. As has been recorded elsewhere (White et al. 2006), eagle attendance at the gull colony varied temporally and peaked during the egg hatching period. Interestingly, we only observed predation of eggs within the non-manipulated plot, which was slightly farther away from the local eagle nest (located ~ 500 m southeast of the study plots) compared to the manipulated plot.

CONCLUSIONS

Gulls in this study did not appear to increase the number of eggs laid to compensate for eggs experimentally removed from their nests. Given the ~ 15 000 Glaucous-winged Gulls breeding on the Copper River Delta (North Pacific Seabird Data Portal 2018), intraspecific competition may be high, thus limiting prey availability. Pressure from subsistence egg harvest in this area appears to be minimal—since its inception in 2014, the number of households in Cordova registered for the subsistence egg harvest, as well as the estimated number of eggs collected, has remained low (100–300 eggs per season, Fig. 3; Naves 2016, AMBCC unpubl. data). Further work on prey availability might reveal the degree of resiliency inherent in the gull populations of the region.

Due to the new harvest pressure in these colonies (i.e., egg harvest has only been legal since 2014), continued research and monitoring is warranted. Future studies should evaluate how varying levels of human disturbance (e.g., group size, time in colony, walking pace) affects the colony and should include methods to track whether gulls re-lay in new nest structures after manipulation.

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REFERENCES


