Simulating the Effects of Predation and Egg-harvest at a Gull Colony

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Abstract

We developed an individual-based simulation model to explore the effects of harvesting eggs from a glaucous-winged gull (*Larus glaucescens*) colony that also experiences egg loss from avian predators. The model has direct application to Glacier Bay National Park, where resource managers are interested in the potential effects of traditional harvesting of gull eggs at colonies within the park. This model simulates the sequence of egg laying, relaying, and incubation to hatching for individual nests and calculates hatching success, incubation length, and total eggs laid in all nests during the simulation. Stochasticity is incorporated in the distribution of nest lay dates, predation rates, and nests attacked during predation and harvest events. We used maximum likelihood to estimate parameters by fitting the model to data collected at South Marble Island in 1999 and 2000. We then simulated harvests and analyzed model predictions. Model outputs suggest that harvesting early, at one time, and from no more than 20 percent of the colony provides a constant harvest with the least impact to gulls.

Introduction

Glaucous-winged gulls (*Larus glaucescens*) are common along the west coast of North America from Washington to the Alaska Peninsula (Verbeek, 1993). Their average clutch size is 3 eggs, and females lay at 2-day intervals until clutches are complete and incubation begins. The loss of all eggs in a nest prior to clutch completion may result in protracted laying, in which case females continue to lay at 2-day intervals until their clutch is complete. Replacing a clutch lost after the onset of incubation requires 12-13 days to resume follicle growth and lay the first egg of the replacement clutch.

Replacement-laying is common in ground-nesting gulls, which have evolved to replace eggs lost to factors such as floods and predators (Brown and Morris, 1996). Common predators of glaucous-winged gull eggs include conspecifics (Verbeek 1988; Good and others, 2000), common ravens (*Corvus corax*) (Patten Jr., 1974) American crows (*Corvus brachyrhynchos*) (Verbeek, 1988) bald eagles (*Haliaeetus leucocephalus*) (Thompson, 1989; Good and others, 2000) and humans (Vermeer and others, 1991). Egg predation by one predator species, such as humans or bald eagles, can also facilitate predation by conspecifics (Hand 1980; Good and others, 2000).

On South Marble Island in Glacier Bay, Alaska, glaucous-winged gull eggs are commonly preyed upon by bald eagles and were traditionally harvested by Huna Tlingit peoples. Little harvesting has been permitted legally in recent decades within Glacier Bay National Park (Hunn and others, 2002). However, the collection of eggs has retained importance as part of the Huna cultural heritage. The goal of this study was to find a balance among the competing interests of gulls, eagles, and people, such as the Huna and the resource managers.

Data collected by Zador (2001) during 2 years at South Marble Island were used to parameterize an individual-based simulation model that predicts hatching success at a gull colony subject to egg loss through predation and harvesting. The model can be used to manipulate the extent and intensity of egg loss in ways that are not possible in the field. Specifically, it can be used to test the effects of variation in timing and intensity of harvest rates given the natural variability in background predation rates.

Methods

An individual-based model was developed that simulates the changes in gull nest contents from pre-laying to hatching. As the simulation proceeds, the status of each nest is updated daily as eggs are laid, lost, replaced, and hatched. The model outputs hatching success (the percent of nests that produce ≥1 chick), the number of eggs laid, the number of eggs harvested, and the length of the simulation (a proxy for the length of the incubation period). The form of the rules on which the simulations were based were determined from field observations at South Marble Island in 1999 and 2000 (Zador, 2001) and glaucous-winged gull biology (Verbeek, 1993). We used maximum likelihood and the field data to estimate parameter values for the distribution of lay dates, the distribution of predation rates, and the probability of replacing eggs in 1999 and 2000. Final clutch sizes (defined as the number of eggs in the nest when incubation begins) are determined by the proportions that were observed in the field. Each simulation run uses parameter values from one of

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the years, chosen randomly. It is assumed that all eggs in a nest are lost during a predation or harvest event and that gull replacement-laying response is the same whether eggs are lost through predation or harvest. Harvest rates are set by specifying the day(s) on which the event is to take place and the percentage of nests in the simulation to be attacked. Our target harvest rate and harvest strategies were based on Huna traditions (Hunn and others, 2002). We analyzed the outcomes of varying harvest strategies relative to each other and to no harvest, and their management implications. In the analysis, Day 1 represents 15 May in 1999 and 14 May in 2000.

Results

Model Fits to Data

A negative binomial distribution, fitted to the observed lay dates in 1999 and 2000, is used to determine the laying dates in the simulations. Lay dates for the nests for each simulation run were drawn randomly from this distribution with an expected mean lay date of 7 June in 1999 and 3 June in 2000. The model randomly determines clutch sizes based on proportions of 3-, 2-, and 1-egg clutches observed in both first clutches and experimentally-forced replacement clutches (table 1). Predation rates declined seasonally. The observed data were modeled by a negative binomial process with mean given by an exponential decline in predation rate with time (0.08 in 1999 and 0.10 in 2000). The daily predation rates were drawn from this distribution as a function of day. Data show that first clutches that were laid later were less likely to be replaced. We fit a logistic model that determined the estimates of the two days on which 95 percent (1999=-4.6, 2000=35.9) and 50 percent (1999=18.8, 2000=45.0) of the lost clutches would be replaced. Replacement probabilities are drawn from this distribution as a function of day. Thus, as each simulation proceeds, clutches that are lost have a decreasing chance of being replaced.

Simulation Results

150 simulations with 100 nests each and no harvest were conducted to determine how well the model performs. The model predicts that with no harvesting, hatching success will be between 64-91 percent, the total number of eggs laid will be between 3.3-4.5 eggs per nest, and the simulation length (a proxy for the incubation period) will be between 71-103 days (fig. 1). Data from 1999 are at the lower end of the range of model predictions, but the model predictions encompass what was recorded at the colony in both years (table 2).

Table 1. The number of eggs in first and replacement clutches (no differences between years). Data from Zador (2001).

	N	3 eggs	2 eggs	1 egg
First clutch	237	199 (84%)	29 (12%)	9 (4%)
Replacement clutch	38	31 (82%)	5 (13%)	2 (5%)

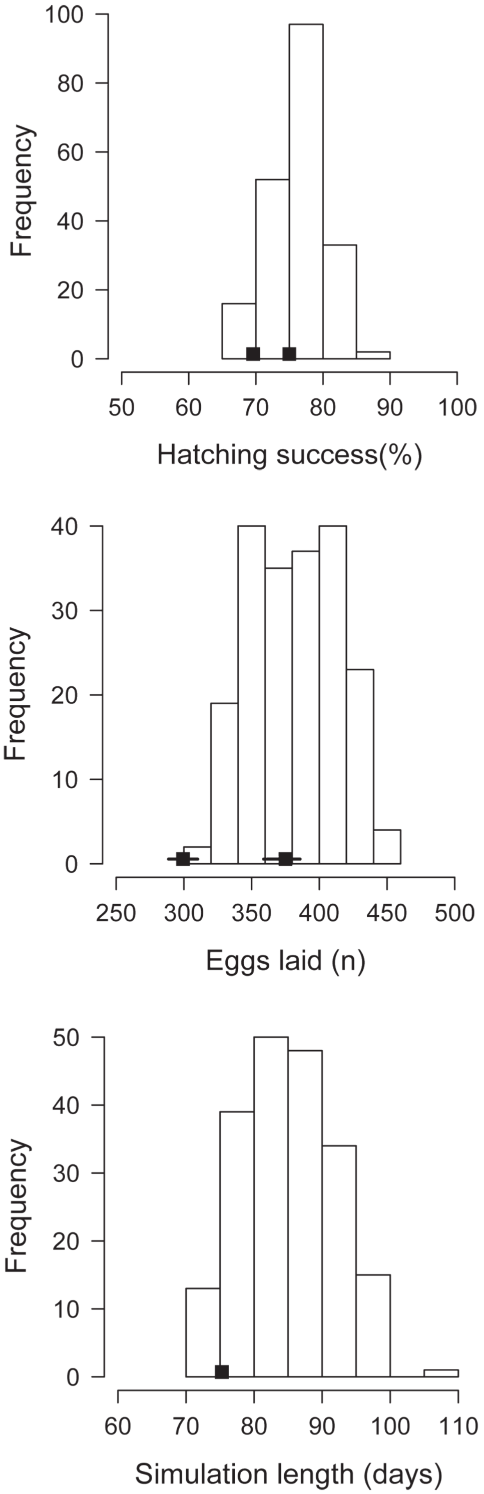

Figure 1. Outputs for 150 simulations with 100 nests each and no harvest. Black boxes show the values observed at nests in 1999 and 2000.

Table 2. Observed outcomes at monitored gull nest plots (mean±S.E.) on South Marble Island. Data from Zador (2001).

	1999	2000
Hatching success	0.75±0.04 (n=135)	0.70±0.04 (n=130)
Eggs laid per nest	3.05±0.09 (n=151)	3.74±0.12 (n=140)
Incubation period		76 days minimum

We chose a target of harvesting from 20 percent of the nests based on traditional harvest practices (Hunn and others, 2002). Given the estimated size of the colony on South Marble Island (500 pairs) and assuming all nests had 3 eggs, this would produce a harvest of approximately 300 eggs. We explored the relative effects of harvesting from 20 percent of the nests on 1 day, over 5 days, or over 10 days. Spreading the harvest over 5 consecutive days reduced the daily harvest to 4 percent, while spreading the harvest over 10 consecutive days reduced the daily harvest to 2 percent. All harvests began on day 20, which corresponds to the first week in June, a traditional time for the Huna to harvest (Hunn and others, 2002). Hatching success varied little among these harvest strategies, and, in fact, differed little from the "no harvest" strategy (fig. 2).

We also explored the relative effects of harvesting from 20 percent of the nests early versus later in the season. Hunn and others (2002) document that some Huna prefer to harvest later for more developed eggs. Hatching success is considerably lower when the harvest is later in the season, due to the decrease in the capacity of gulls to lay replacements (fig. 3). The number of eggs harvested also tends to be reduced slightly when the harvest is later in the season.

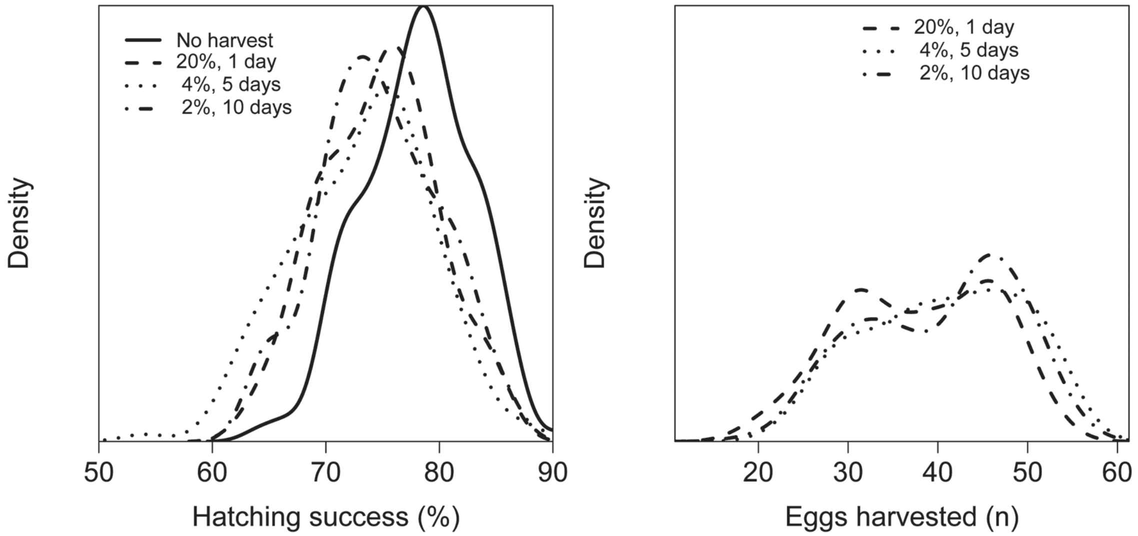

Figure 2. Sensitivity of hatching success (left) and number of eggs harvested (right) to the number of days over which harvest occurs. Plots show kernel density estimates such that the area under each curve integrates to 1.

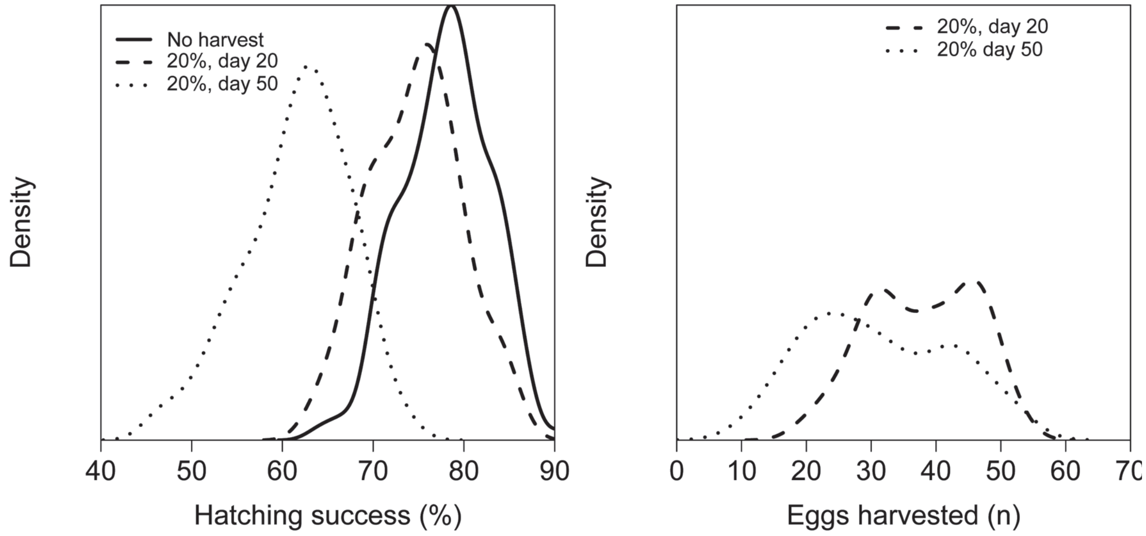

Figure 3. Sensitivity of hatching success (left) and number of eggs harvested (right) to whether a harvest of 20% of nests occurs early or late during the incubation period. Plots show kernel density estimates such that the area under each curve integrates to 1.

Discussion and Conclusions

The simulations involved selecting randomly between behavior based on the 1999 observations and the 2000 observations for each run rather than on an average of the observations for those years to retain the variability seen in lay dates, predation rates, and replacement probabilities among years. The probability distributions chosen for lay dates, predation rates and replacement probabilities then capture within-year variability. In running projections based on such limited data, it is important to retain stochasticity so that model predictions are not based on exact replicas on what occurred in 1999 and 2000. Model predictions were accordingly broad, but realistic. The length of the simulations further supports this by predicting appropriate incubation period lengths, in other words not having gulls continue to lay eggs though September. Although eagles were the main egg predators during the field study, there were likely other sources of egg loss that are not included in this model, which may help explain why model predictions tended to be higher than what was observed. However, even without the inclusion of additional mortality, the relative effects of varying harvest strategies remain informative.

Gulls are apparently able to replace eggs in such a way that does not compromise their hatching success whether a set target (20 percent) is harvested all on one day or spread out over several consecutive days. More eggs are likely harvested with the intermediate strategy (harvesting 4 percent over 5 days), as there are more eggs per nest as the season progresses. However, spreading the harvest out also increases the human disturbance at the colony, which can also ultimately lead to decreased hatching success via elevated predation. In addition, conducting harvests on one day increases the replacement laying synchrony among gulls, which itself decreases each individual nests' exposure to predation. If the harvest is constrained to one day but later in the season, the total harvest is larger because most nests will have complete clutches. However, hatching success is lower because eggs are less likely to be replaced when lost later in the incubation period.

Management Implications

We took a simulation approach to understanding the effects of harvesting in a situation where it was not possible to test a variety of harvest strategies in the field. Accordingly, our model incorporates uncertainty in its estimates, which is necessary when any management plan is based on limited data. However, combining the results of our simulations with what is known about gull biology allows us to make both short-term and long-term recommendations. In the short-term, based on data collected in 1999 and 2000, harvesting early in the breeding season and harvesting at one time would minimize impact on populations. This strategy has the least impact to gull reproductive output both directly (greater probability of replacing harvest eggs) and indirectly (by reducing disturbance and increasing breeding synchrony). Over the longer term, gull populations should be monitored annually, as population size is the ultimate concern of the managers. Predation should be monitored to see if the levels of eagle predation seen in 1999 and 2000 continue or if other predators (such as river otters) impact the system. In addition, if vegetative succession continues at the pace that it has since the island was exposed from a retreating glacier, the forest which currently covers half of the island will likely expand. As this occurs, the amount of open area that serves as nesting habitat for the gulls will likely decrease. Reduction in nesting habitat can lead to a breeding population decline. Finally, we emphasize that it is important to understand the potential influences on gull population trends so that harvest management plans can be adjusted in an adaptive manner.

Acknowledgments

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Researchers measure the abundance of intertidal invertebrates that serve as food for various nearshore predators. (Photograph by Brenda Ballachey, U.S. Geological Survey.)