Balancing predation and egg harvest in a colonial seabird: A simulation model

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ABSTRACT

We developed an individual-based model to study the effects of different regimes of harvesting eggs and natural predation on reproductive success in a colony of the glaucous-winged gull (*Larus glaucescens*) in Glacier Bay National Park, Alaska. The model incorporates the sequence of egg laying, relaying, and incubation to hatching for individual nests and calculates hatching success, incubation length, and the total number of eggs laid (as a result of re-nesting and relaying) in all nests in the colony. Stochasticity is incorporated in the distribution of nest lay dates, predation rates, and nests attacked during predation and harvest events. We estimated parameter values by fitting the model to data collected at a small colony during 1999 and 2000 using maximum likelihood. We then simulated harvests and analyzed model predictions. Model outputs indicate that harvesting early, and at one time, provides a predictable take of eggs with the least impact to gulls.

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1. Introduction

On South Marble Island in Glacier Bay, Alaska, eggs of the glaucous-winged gull (*Larus glaucescens*) are commonly preyed upon by the bald eagle (*Haliaeetus leucocephalus*) and are traditionally harvested by Huna Tlingit peoples. Little legal harvesting has been permitted in recent decades within Glacier Bay National Park (Hunn et al., 2003), but the collection of eggs is an important part of Huna cultural heritage. We developed a simulation model to evaluate the impact of various harvest scenarios, based on data collected from two field seasons in Glacier Bay (Zador, 2001). This model could be used to form the basis for a reconciliation between conservation of gulls and the needs of the Huna Tlingit peoples.

Replacement laying is common among ground-nesting gulls, the capacity having evolved to replace eggs lost to factors such as floods and predators (Brown and Morris, 1996), and is key to selecting an appropriate harvest strategy based on conservation and harvest goals. Common predators of the eggs of glaucous-winged gulls include conspecifics (Verbeek, 1988; Good et al., 2000), common ravens (*Corvus corax*) (Patten, 1974), American crows (*Corvus brachyrhynchos*) (Verbeek, 1988), bald eagles (Thompson, 1989; Good et al., 2000), and humans (Vermeer et al., 1991). Egg predation by one predator species, such as humans or bald eagles, can also facilitate predation by conspecifics (Hand, 1980; Good et al., 2000).

Glaucous-winged gulls are common along the west coast of North America from Washington to the Alaska Penin-

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sula (Verbeek, 1993). Their average clutch size is three 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 clutches are 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.

The goal of this study was to see if a balance could be found among the competing interests of gulls, eagles and people in the National Park. However, the model has application to other similar cases where eggs are harvested by indigenous peoples, e.g., sooty terns (*Sterna fuscata*) and brown noddies (*Anous stolidus*) in the tropics and alcids in the Arctic and sub-arctic (Feare, 1976; Haynes, 1987; Gaston and Jones, 1998). Historically, egg harvesting from colonial seabirds has been part of various cultures (Burger and Gochfeld, 1994). Indeed, harvesting has occurred wherever human populations have had access to eggs of breeding seabirds. Egg harvesting has been identified as a threat to some seabird populations (Haynes, 1987; Burger and Gochfeld, 1994) and attributed to the decline of others (Ainley and Lewis, 1974; de Juana, 1984). Collecting or destroying eggs has been used as a management technique with success to reduce gull population sizes (Wanless et al., 1996; Ickes et al., 1998). However, managed egg harvests may also present conservation benefits by increasing the value, and thereby protection, of the resource (Feare et al., 1997). To date, few studies have specifically considered outcomes of a managed egg harvest (but see Feare, 1976; Haynes, 1987).

Individual-based simulation models have been used in a variety of cases to explore the effects of predation and mortality on vertebrate populations (Richards et al., 2004; Seymour et al., 2004). In this paper, data collected by Zador (2001) were used to parameterize an individual-based model tailored to the glaucous-winged gull that predicts the overall hatching success at a gull colony that is subjected to egg loss through predation and harvesting. The model we developed was used to manipulate the extent and intensity of egg loss. Specifically, it was used to examine the effects of variation in timing and intensity of harvesting given the natural variability in background predation rates. Different scenarios were simulated to seek the one allowing highest hatching success.

2. Methods

2.1. Model overview

We developed an individual-based model implemented using the R language (R Development Core Team, 2005) 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. For each simulation, the model outputs hatching success (the percent of nests that produce at least one 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).

Table 1 – The numbers of 3-, 2-, and 1-egg clutches (and percentage of total) observed in first and experimentally-forced replacement clutches

	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)

Source: Zador (2001). Values in parenthesis are in percentage.

2.2. Model structure

The rules on which the model is based were determined from field observations at South Marble Island in 1999 and 2000, when nest contents were recorded every 1–2 days from pre-laying through chick hatching (Zador, 2001), as well from the literature, e.g., on glaucous-winged gull biology (Verbeek, 1993).

(1) *Egg-laying sequence*. One egg is laid on the initial laying date for each nest. An additional egg is laid every other day until the final clutch size is reached. The model randomly determines final clutch sizes (defined as the number of eggs in the nest when incubation begins) based on proportions of 3-, 2-, and 1-egg clutches observed in both first clutches and experimentally forced replacement clutches (Table 1). The nest contains these eggs each subsequent day, simulating incubation, until the eggs hatch or are taken by predators or harvesters.

(2) *Hatching*. On the 27th consecutive day that the nest has contained a clutch, all eggs hatch and the simulation for that nest is complete.

(3) *Egg loss*. On a day that a predator or harvester targets a nest, all eggs are removed from that nest.

(4) *Replacing eggs lost during the egg-laying sequence*. Eggs taken by predators or harvesters during the egg-laying period, before the final clutch has been laid, are replaced in a way that mimics protracted laying. The nest remains empty for 1 day after predation. On the next day, the nest contains one egg and the egg-laying sequence resumes.

(5) *Replacing eggs lost during incubation*. Eggs that are taken by predators or harvesters once the clutch is completed and incubation begins (the nest contains the entire clutch) are replaced after a period that mimics the time required for the female to produce new eggs. The nest remains empty for 11 days after loss, and on the 12th day, the nest contains one egg and the egg-laying sequence resumes, as above.

(6) *Stopping rules*. When a nest has contained six eggs in total or two complete clutches and loses its eggs to a predator or harvester, the eggs are not replaced. The breeding attempt at that nest is considered failed.

It is therefore assumed that all eggs in a nest are lost during a predation or harvest event and that the 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 harvesting event is to take place and the percentage of nests in the simulation to be attacked. The target harvest rates and harvest strategies (e.g., when to harvest) were based on Huna traditions (Hunn et al., 2003). We ana-
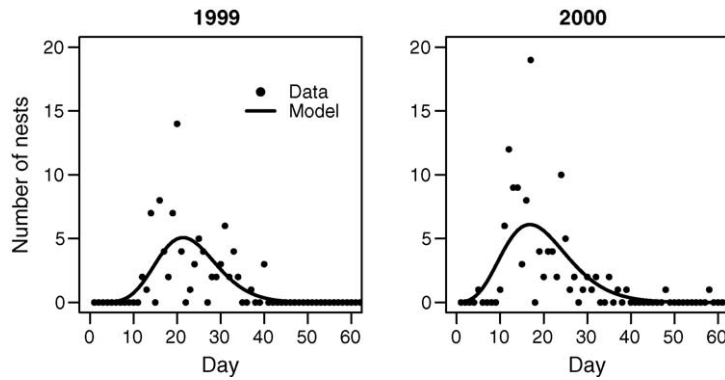
Fig. 1 – Fit of the negative binomial distribution to the observed lay dates of gulls in 1999 ($n = 151$) and 2000 ($n = 140$). Data from Zador (2001).

lyzed the outcomes of harvest strategies relative to each other and to a scenario of no harvest. In the analysis, day 1 of the simulation represents 15 May in 1999 and 14 May in 2000.

2.3. Parameter estimates

The model was fitted to data collected at South Marble Island in 1999 and 2000 (Zador, 2001). Maximum likelihood was used to estimate parameter values for the distribution of lay dates, the distribution of predation rates, and the probability of replacing eggs separately for 1999 and 2000. Representing these processes using distributions allowed investigation of the effects of stochascity in population processes on the model outputs. Also, fitting data from each year separately, rather than as an average, retained the annual variability seen in the data. Each simulation used all parameter values from one of the years, chosen randomly.

3. Results

3.1. Model parameterization

Negative binomial distributions, fitted to the observed lay dates in 1999 and 2000 (Fig. 1), were used to determine laying phenology. The lay date for each nest was therefore drawn randomly from the distributions in Fig. 1 (expected lay date from

day 0: 23.0 in 1999 and 19.5 in 2000; overdispersion parameter: 20.6 in 1999 and 8.9 in 2000). Predation rates (the number of nests attacked per nest with eggs) declined over the season (Fig. 2). The daily predation rate was therefore drawn from negative binomial distributions (one for each of 1999 and 2000) where the expected predation rate declines exponentially with time, i.e.:

$$P_d = P_0\, e^{-\lambda d} \tag{1}$$

where P_d is the predation rate on day d and λ is rate at which predation rate declines with time (0.08 for 1999; 0.10 for 2000). The overdispersion parameters of the two negative binomial distributions were set to 100 because the data were highly overdispersed.

Data show that first clutches that are laid later in the season are less likely to be replaced (Fig. 3). The daily probability of a nest being replaced following predation or harvest was drawn from a binomial distribution where the expected probability of replacement declines as a logistic function of time, i.e.:

$$P\,(\text{renest}) = \left(1 + \exp\left(-\ln 19 \left\{\frac{d - p_{50}}{p_{95} - p_{50}}\right\}\right)\right)^{-1} \tag{2}$$

where p_{50} and p_{95} are, respectively, the days on which there is a 50 and 95% probability of a nest being replaced (p_{50}: 18.8 and
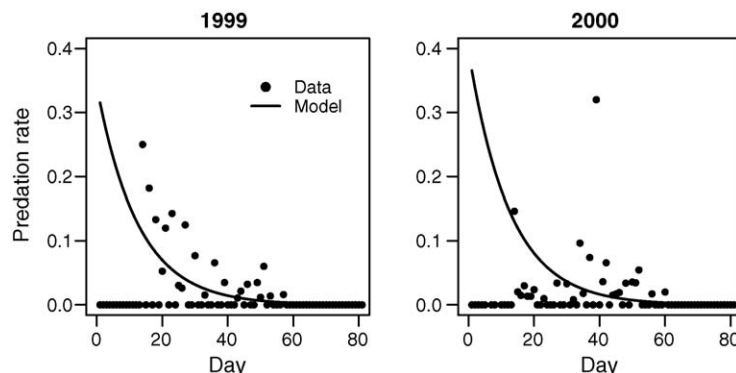

Fig. 2 – Exponential model fits to observed daily predation rates. The high point in 2000 represents a day on which 32% of the nests were attacked.
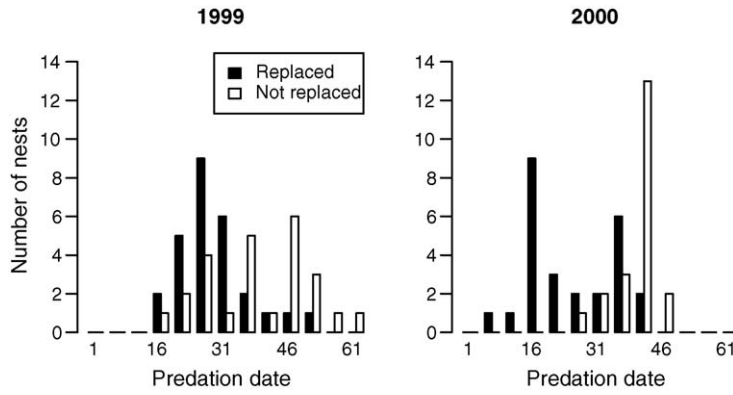
Fig. 3 – The number of nests that were depredated and whose eggs were later replaced (solid) and not replaced (white).
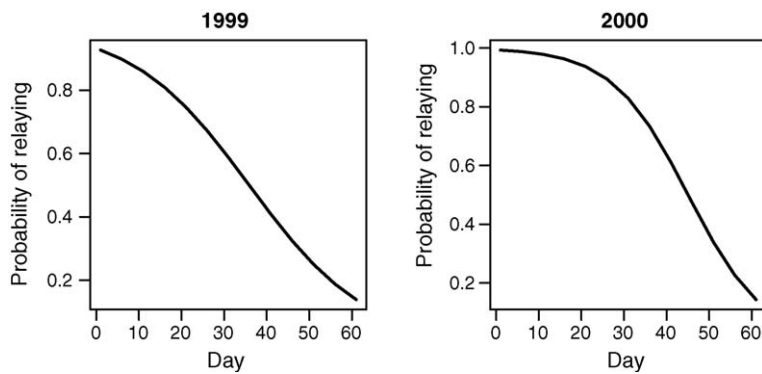

Fig. 4 – Probability of replacing eggs as a function of day during the season.

45.0 for 1999 and 2000; p_{95}: −4.6 and 35.9 for 1999 and 2000; Fig. 4).

3.2. Selecting the number of nests and simulations

Analysis of variance applied to hatching success and the number of eggs laid found no significant differences among simulations involving 50, 100, and 200 nests when there was no harvest (hatching success: $F = 0.202$, $p = 0.653$; eggs laid: $F = 2.892$, $p = 0.090$; $n = 100$ simulation runs; Fig. 5). Fig. 6 shows the variance in hatching success and in the number of eggs laid as a function of the number of simulations. Variance in hatching success remained unchanged after about 200 simulations while that in the number of eggs laid remained unchanged after about 50 simulations. Therefore, 100 nests and 200 simulations represented an appropriate compromise between low variance and computing speed.

3.3. Simulation results

Simulations with no harvest were conducted to determine how well the emergent behavior of the model mimics reality.
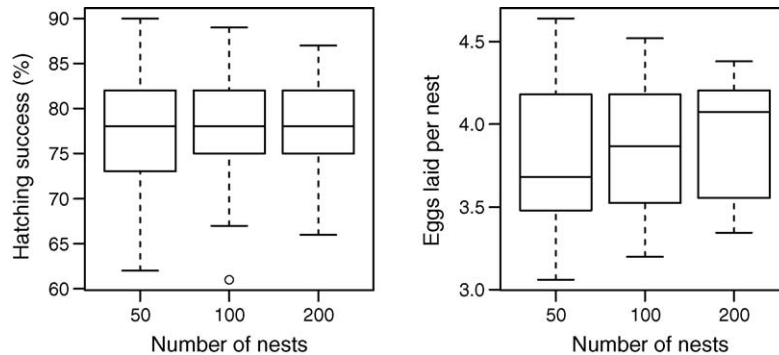

Fig. 5 – Boxplots for estimated hatching success (left) and number of eggs laid (right) when the number of nests in the simulation varied from 50 to 200 and there was no harvest. Boxes show the interquartile ranges and median values. Whiskers extend to the extreme values of the data or 1.5 times the interquartile range, whichever is less. The circle indicates an outlier.
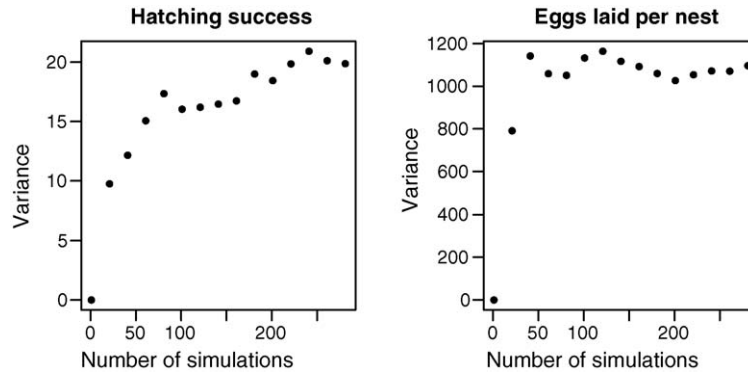
Fig. 6 – Variance in hatching success (left) and in the number of eggs laid (right) as a function of the number of simulations. All simulations were based on 100 nests and no harvest.

The model predicts that with no harvesting, hatching success will be between 64 and 91%, the total number of eggs laid will be between 3.3 and 4.5 eggs per nest, and the simulation length (a proxy for the incubation period) will be between 71 and 103 days (Fig. 7). The number of eggs laid in 1999 is at the lower end of the range of model predictions, but the model predictions nevertheless encompass what was recorded at South Marble Island in both years (Table 2).

We chose to focus on a harvest of 20% of the nests (based on traditional harvest practices; Hunn et al., 2003). We explored the relative effects of harvesting from 20% 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%, while spreading the harvest over 10 consecutive days reduced it to 2%. All harvests began on day 20, which corresponds to the first week in

Table 2 – Observed outcomes at monitored gull nests (mean ± 1S.E.) on South Marble Island		
	1999	2000
Hatching success	75% ($n = 135$)	70% ($n = 130$)
Eggs laid per nest	3.05 ± 0.09 ($n = 151$)	3.74 ± 0.10 ($n = 140$)
Incubation period		At least 76 days
Source: Zador (2001).		

June, a traditional time for the Huna to harvest (Hunn et al., 2003). Hatching success and the number of eggs harvested varied little among these harvest strategies, and, in fact, differed little from the "no harvest" strategy (Fig. 8).
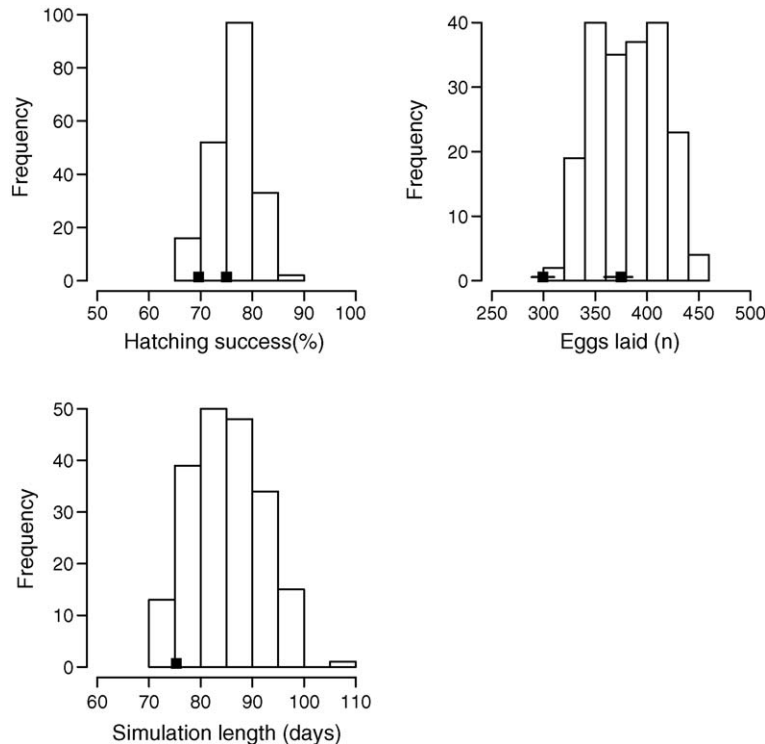

Fig. 7 – Outputs for 150 simulations with 100 nests and no harvest. Black boxes show the values observed at nests in 1999 and 2000 (see Table 2).
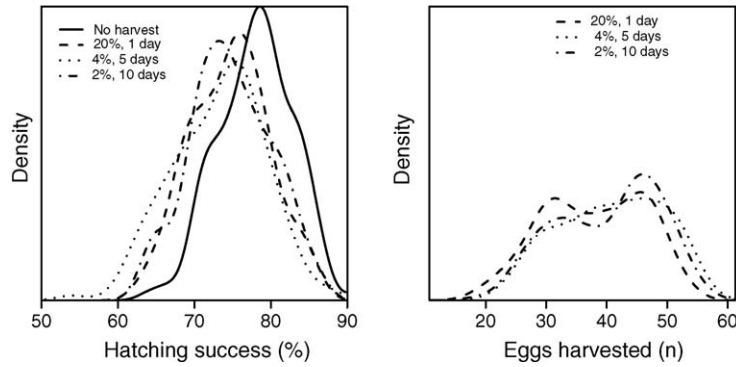
Fig. 8 – Sensitivity of hatching success (left) and number of eggs harvested (right) to the number of days over which harvest occurs. Plots show kernel density estimates with a Gaussian kernel such that the area under each curve integrates to 1.
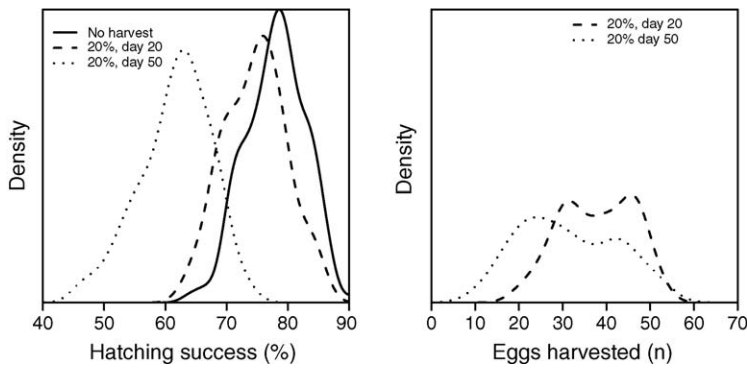

Fig. 9 – Sensitivity of hatching success (left) and number of eggs harvested (right) to whether a harvest of 20% of nests occurs early or late during the incubation period. Plots show kernel density estimates with a Gaussian kernel such that the area under each curve integrates to 1.

The relative effects of harvesting from 20% of the nests early versus later in the season is explored because Hunn et al. (2003) document that some Huna prefer to harvest later for more developed eggs. Fig. 9 compares a strategy in which 20% of the nests are harvested on day 50 with that in which 20% of nests are harvested on day 20. Hatching success is considerably lower when the harvest is later in the season, owing to a 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.

Hatching success changes little if the harvest rate on day 20 is increased from 20 to 100% (Fig. 10). The number of eggs harvested increases as the harvest rate increases to 40%, but remains unchanged at higher harvest rates. These patterns are explained by the laying phenology of the gulls. On day 20 fewer than half of the nests contain eggs, and the effects of harvest

Fig. 10 – Sensitivity of hatching success (left) and number of eggs harvested (right) to the percentage of nests that are harvested from early in the incubation period (day 20). Plots show kernel density estimates with a Gaussian kernel such that the area under each curve integrates to 1.
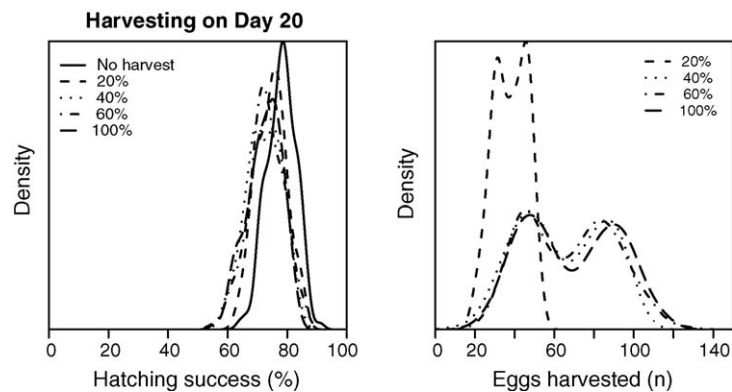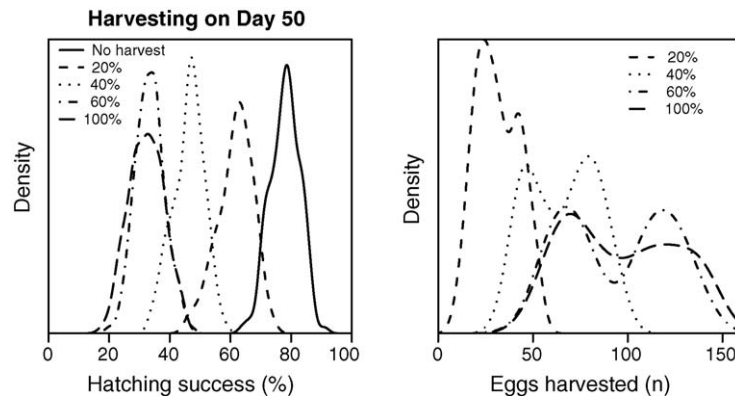
Fig. 11 – Sensitivity of hatching success (left) and number of eggs harvested (right) to the percentage of nests that are harvested from late in the incubation period (day 50). Plots show kernel density estimates with a Gaussian kernel such that the area under each curve integrates to 1.

reach their maximum at a 40% harvest rate. However, if harvests are increased later during the season (on day 50), the effects on hatching success and the number of eggs harvested is stronger (Fig. 11). Hatching success declines and the number of eggs harvested increases as the harvest rate increases, but the number of eggs harvested reaches the maximum at a 60% harvest rate. This reflects the fact that by day 50, some of the earlier nests have finished for the season and are therefore not available for harvest.

4.   Discussion

Our approach differs from previous seabird egg harvest management studies by using simulations to explore harvest management scenarios (Feare, 1976; Haynes, 1987). The simulations involved selecting randomly between behavior observed in 1999 and 2000, rather than averaging observations over years to estimate the parameter values (Figs. 1, 2 and 4) because this mimics the observed variability 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 this relatively limited data set, it was important to retain stochasticity so that model predictions were not based on exact replications of what occurred during 1999 and 2000. Model predictions were accordingly broad, but realistic. For example, the length of the simulations predicted appropriate incubation periods, i.e., gulls did not continue to lay eggs though September which would be unrealistic. Although an attempt has been made to capture among-year variation in population parameters, the extent to which the results correctly capture long-term behavior depends on the extent to which 1999 and 2000 are representative of future conditions. There are no reasons to suggest that these years are unrepresentative of future conditions, but this possibility cannot be ruled out altogether either.

Although eagles were the main egg predators during the field study, there may have been other sources of egg loss that are not included in the model (e.g., loss due to conspecifics or investigator disturbance), which may help explain

why the model predictions tended to be higher than what was observed in the field. However, even without including these additional sources of mortality, the relative effects of the different harvest strategies are informative.

Gulls are apparently able to replace eggs in such a way that does not compromise their hatching success regardless of whether 20% of the nests are harvested all on 1 day or the harvest is spread over several consecutive days. However, spreading the harvest also increases the disturbance at the colony, which could also ultimately lead to decreased reproductive success (Brown and Morris, 1995; Sullivan et al., 2002; Hothem and Hatch, 2004). Also, nests may be visited more than once during a harvest conducted over several days, increasing the chance that the gulls will fail to replace eggs (Vermeer et al., 1991). In contrast, conducting harvests on 1 day increases the replacement-laying synchrony among gulls, which itself decreases each individual nests' exposure to predation. Conducting the entire harvest on 1 day rather than over several days appears to have the least negative impact on the gulls and little effect on the number of eggs harvested.

If harvesting occurs early during the season, increasing the size of the harvest has little effect on hatching success because only a small portion of the nests have eggs at that time and most gulls that lose eggs are then able to replace them. In contrast, harvesting from relatively few nests later in the season will depress hatching success. At that time, fewer gulls are able to replace their eggs because many have already reached a physiological limit to the number of eggs or clutches they can lay. Increasing the harvest rate late in the season further decreases hatching success, until only those early nests that hatched out before the harvest are successful. At the same time, the number of eggs harvested increases until all nests with eggs have been harvested. In summary, harvests conducted later in the season can yield more eggs than similar efforts conducted earlier in the season, but hatching success is much reduced because gulls are less likely to replace eggs lost later in the season.

The model predictions can help resource managers to design an egg harvest plan. The model suggests that managers should exert more control over the timing (better earlier) and number (better few) of harvesting events rather that the

overall harvest rate (number of nests visited) for two reasons. First, it is logistically simpler to control access to the island by regulating the days on which harvesters may visit rather than trying to control and monitor visits to individual nests. Second, by constraining the timing of the harvest to a day(s) early in the season, the impact on reproductive success of the gulls is low. While it is possible to devise an egg harvest plan for minimal impact, managers cannot control other factors such as food supply, predation, or habitat quality that all influence gull reproductive success and, ultimately, population trends (Verbeek, 1993). Gull colonies in Glacier Bay have shifted in size and distribution during the past ca. 200 years (Zador and Piatt, unpublished data), and so it would be prudent to evaluate and adapt the harvest management plan on a regular basis.

Although this model was developed for a specific case study, it could be applied in different areas or to different species where it is important to make egg harvest traditions and conservation compatible. The model would be most suited to species whose breeding biology was well known (as is the case for many gulls and terns) and where variability in the source(s) of nest loss (such as predation) can be measured or estimated. In addition to egg harvests, this approach could be used to explore management schemes for harvests of seabird chicks, for example, the traditional Maori harvest of sooty shearwaters (*Puffinus griseus*) (Kitsen, 2002).

5.   Conclusions

A simulation approach was used to understand the effects of egg harvesting in a situation where it was not possible to test harvest strategies in the field. To increase model realism, Van Nes and Scheffer (2005) suggest going beyond simple differential equation models (Jensen, 2001; Watola et al., 2003). The model described here incorporates some complexity not easily captured by simpler models by including individual-based processes. It also captures uncertainty, which is vital given the limited data (Hilborn and Walters, 1992). Combining our results of simulations with what is known about gull biology allowed formulation of both short-term and long-term management recommendations.

In the short-term we recommend harvesting early in the breeding season and harvesting at one time. This strategy has the least impact on reproductive output both directly (greater probability of replacing harvested eggs) and indirectly (by reducing disturbance and increasing breeding synchrony). Over the longer term, we recommend annual monitoring of the gull population, as both the harvest and management of populations depend on census data. We also recommend monitoring predation to see if the levels of eagle predation seen in 1999 and 2000 continue or if other predators (such as river otters *Lutra canadensis*) impact the system (Vermeer and Devito, 1989). In addition, if vegetative succession continues at the pace that it has since the island was deglaciated, the forest which currently covers half of South Marble Island will likely expand (Glacier Bay National Park, unpublished data). This monitoring is necessary because the amount of open area that serves as nesting habitat for the gulls will inevitably decrease which may in turn lead to a decline in the size of a breeding

population (Erwin et al., 2003). Finally, we emphasize that it is essential to measure other potential influences on gull populations so that harvest plans can be adjusted in an adaptive manner if egg harvesting is permitted.

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