

The background of the entire page is a photograph of a bird's nest. The nest is constructed from a dense layer of dry, brown pine needles and twigs. Three large, oval-shaped eggs are the central focus. They have a light, yellowish-green base color with numerous dark brown and black spots and blotches of varying sizes. The eggs are arranged in a triangular pattern: one at the top, one at the bottom left, and one at the bottom right. The lighting is natural, highlighting the texture of the eggs and the surrounding nesting material.

**SIMULATING THE EFFECTS OF PREDATION  
AND EGG-HARVEST AT A GULL COLONY**

**Final Report to:  
Glacier Bay National Park  
Gustavus, Alaska**

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RH: Egg-harvest simulation model • *Zador and Piatt*

**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 concerned about potential negative effects of traditional Native Alaskan harvesting of gull eggs at colonies within the park. The model simulates the sequence of egg laying, relaying, and incubation to hatching for individual nests and calculates hatching success, incubation length, total egg harvest, and total eggs laid in all nests during the simulation. Stochasticity is incorporated in the

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distribution of nest lay dates and in the number of nests attacked during predation and harvest events. Model outputs suggest that (1) harvest strategies are largely ineffectual when background predation rates are high, and, (2) harvesting early, at one time, and from no more than 20% of the colony provides a constant harvest with the least impact to gulls when background predation rates are low to moderate (and within the natural range observed in the field).

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**Key words:** egg-harvest, Glacier Bay, glaucous-winged gull, *Larus glaucescens*, predation, simulation.

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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 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 et al 2000), common ravens (*Corvus corax*) (Patten Jr 1974) American crows

(*Corvus brachyrhynchos*) (Verbeek 1988) bald eagles (*Haliaeetus leucocephalus*) (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).

On South Marble Island in Glacier Bay, Alaska, glaucous-winged gull eggs are commonly preyed upon by bald eagles and harvested by native peoples. The harvest of seabird eggs is a traditional subsistence activity of the Tlingit peoples in southeast Alaska, but little harvesting has been permitted legally in recent decades within Glacier Bay National Park (Hunn et al 2002). Historically, eggs were an important source of fresh food for the Tlingit peoples because they were available early in the spring before many other foods. Today, the collection of eggs has retained importance as part of the Tlingit cultural heritage. The goal of this study was to find a balance among gulls, eagles and people that would allow egg harvests to be managed against the background of natural predation.

We documented the nesting activities of gulls on South Marble Island for two years and used these data to construct a simulation model that predicts hatching success at a gull colony subject to egg loss through predation and harvesting. The model allowed us to manipulate the extent and intensity of egg loss in ways that were not possible in the field study. Specifically, it allowed us to test effects of variation in timing and intensity of harvest rates against a range of natural background predation rates.

## STUDY AREA AND METHODS

South Marble Island is a ~5 ha rocky island in Glacier Bay National Park, Alaska (58°39'N 136°0'W). Approximately 500 pairs of glaucous-winged gull nest on its exposed cliffs and grassy slopes. During 1999 and 2000, we monitored the nesting activities of 158 and 140 gull pairs, respectively. We checked nest contents every 1-4 days from pre-laying until chicks hatched, and recorded all egg loss and replacement. Based on direct observation, we determined that bald eagles were the cause of most egg predation. Because we observed no conspecific predation, we assumed that it occurred rarely and so had little influence on the laying patterns of the gulls.

We designed an individual-based model that simulates the changes in gull nest contents during the course of a breeding season (e.g., Fig. 1). The program is written in the S-PLUS programming language. The number of nests, predation rate, and harvest rate are set at the beginning of each simulation. All nests are empty at the start of the simulation (Fig. 1). As the simulation proceeds, the status of each nest is updated daily as eggs are laid, lost, replaced and hatched. Stochasticity is incorporated in the distribution of initial laying dates for each nest and the distribution of attacks on days of predation and harvest events. The simulation ends when all nests have hatched or will no longer replace lost eggs. We consider the number of days from the beginning to end of the simulation to be the length of the egg period (Fig. 1), a colony-level measure of the time from egg-formation to the end of hatching. Each simulation of the model run under different scenarios (e.g., Fig. 1) allows us to calculate hatching success (the percent of

nests that hatched eggs from all nests in the simulation), the length of the egg period, the total number of eggs harvested, and the total number of eggs laid.

Rules for the model structure are based on published data of glaucous-winged gulls (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 nest contains 3 eggs. The nest contains 3 eggs each following day, simulating incubation, until the eggs hatch or are taken by predators or harvesters. (2) *Hatching*. On the 27<sup>th</sup> consecutive day the nest has contained 3 eggs, all eggs hatch and the simulation for that nest is complete. (3) *Egg loss*. On the day a predator or harvester targets a nest that contains eggs, all eggs are removed from that nest. (4) *Replacing eggs lost during the egg-laying sequence*. Eggs that are taken by predators or harvesters during the egg-laying period, when the nests contain 1 or 2 eggs, 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 1 egg and resumes the egg-laying sequence. (5) *Replacing eggs lost during incubation*. Eggs that are taken by predators or harvesters during the incubation period, when the nest contains 3 eggs, 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 predation. On the 12<sup>th</sup> day, the nest contains 1 egg and resumes the egg-laying sequence. (6) *Stopping rules*. When a nest has contained 8 eggs in total or 2 complete clutches and loses its eggs to a predator or harvester, the eggs will not be replaced. The breeding attempt at that nest is considered failed for that simulation.

The model includes 4 parameters: the distribution of lay dates, the predation rate, the number of nests, and the harvest rate. The initial laying date for each nest ( $x$ ) is drawn with replacement from a list comprising 100,000 values derived from

$$x = \text{rnorm}(((12,3)^{1.8})/10)$$

where  $x$  is a random value drawn from a normal distribution with a mean of 12 and a standard deviation of 3. This distribution follows the distribution of initial laying dates of the 50 nests chosen randomly from nests we monitored in 1999. We used this distribution in all simulations. Predation rates are expressed as the proportion of the number of nests in the simulations to be attacked daily. For example, in simulations with 50 nests, when the predation rate is 0.001, 1 nest is attacked every 20 days while at a rate of 0.095, 6 nests are attacked per day. 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.

We conducted sensitivity analyses of the number of nests in the simulation, the number of simulations, and the predation rates. We compared the variance in hatching success and simulation length among simulations of 10, 50, and 100 nests with a constant predation rate of 0.015 and no harvest ( $n = 10$  sets of 50 simulations at each level). We chose to use 50 nests in all subsequent simulations as a compromise between low variance and computing speed. To determine how many simulations to run, we compared variances in hatching success and length of the egg period in simulations run 10 to 225 times. After 150 simulations, variances remained unchanged, so we chose to run subsequent simulations 150 times for each combination of parameter values. First, we ran simulations with no predation. Then, we tested the range of predation rates (0.001 to 0.095) that caused near complete hatching success or failure. Finally, we examined these simulation effects on all other model outputs.

To evaluate how well model outputs compared with nesting activities at real gull nests, we used data collected from 108 nests in 1999 and 140 nests in 2000 on South

Marble Island to calculate daily predation rates in each year. We considered these nests to be reference nests; they do not include the 50 nests from 1999 that we used to derive the initial laying dates. Using these natural predation rates in our model, we simulated egg production and compared model outcomes with outcomes observed in the field.

To assess the effects of human harvest on egg production, we inputted varying harvest schedules, timing of harvests and amounts of harvest and we then compared model outputs. We chose to test harvest strategies that resembled those recounted in the oral history of the Huna Tlingit (Neal 1999, Hunn et al 2002). Most strategies were based on a target of harvesting from 20% of the nests (an extrapolation of 300 eggs gathered from a 500-nest colony) on the 15th day of the simulation (phenologically equivalent to the first week of June, the traditional harvest time). All harvest strategies were tested against a range of background predation rates.

Statistics were computed with S-PLUS (S-PLUS 2000, Mathsoft Inc.) and SPSS (SPSS for Windows v. 9, SPSS Inc.). We tested all datasets for normality and used parametric statistics throughout. Hatching success values were arcsine-transformed for analysis of variance (ANOVA). We used 1-way ANOVA to test the effects of predation and 2-way ANOVAs to test the effects of predation and harvest on model outputs. For post-hoc tests we used Tukey's Honestly Significant Difference. We consider differences to be significant at the 0.05 level. All means are reported  $\pm 1$  se.

## **RESULTS**

### **Effects of predation**

In simulations run with the lowest predation rate (0.001), 1 nest was attacked every 20 days; whereas at the highest rate (0.095), 6 nests were attacked daily. Increasing the



predation rate decreased hatching success (Fig. 2,  $F = 46315$ ,  $df = 6$ ,  $P < 0.001$ ). The greatest declines in hatching success occurred as predation changed from an episodic to a daily event (at 0.005 and 0.015, respectively). As the number of nests that were attacked each day increased, <21% of nests successfully hatched. When the predation rate was 0.095, >99% of nests failed to hatch any chicks.

With no predation, the mean length of the egg period was  $50.76 \pm 0.25$  days (Fig. 1). When predation was initially introduced, the length of the egg period increased markedly to greater than 65 days (Fig. 2). The egg period was longest when predation events occurred infrequently, reflecting the time needed to replace clutches. As predation rates increased beyond minimal, however, the length of the egg period decreased ( $F = 352$ ,  $df = 6$ ,  $P < 0.001$ ). When predation events occurred 6 times per day, the mean length of the egg period fell below 50 days as most gull pairs quickly reached the limit of eggs they could replace.

With no predation, pairs laid and incubated 3 eggs to hatching. When predation was introduced, greater numbers of eggs were laid to replace those lost ( $F = 17093$ ,  $df = 6$ ,  $P < 0.001$ ). The maximum numbers of eggs were laid ( $361.68 \pm 0.87$ ) when predation rates were 0.075. Post-hoc analysis showed that when predation rates were higher, the total numbers of eggs laid declined ( $P < 0.001$ ).

### **Comparing model predictions to reference nests**

The average daily predation rates in the reference nests were 0.007 in 1999 and 0.009 in 2000. When we input these rates into the model, it predicted higher hatching success and total numbers of eggs than we actually observed in the reference nests (Table 1). In 1999, hatching success was 23% lower than predicted, and in 2000, hatching success was

5% lower than predicted. These differences were expected because nests in the simulations lost eggs only because of predation, whereas some of the reference nests failed to hatch eggs because of other factors (such as infertility, mortality, crushing, etc.). Similarly, 35 fewer eggs were laid in 1999 than predicted, and 15 fewer eggs were laid in 2000 than predicted. The model assumed that all pairs laid 3-egg clutches, but some of the reference pairs laid only 1 or 2-egg clutches, resulting in fewer total numbers of eggs than were predicted.

### **Harvest analysis**

*Harvest schedules.*-- Overall, predation had a greater influence on hatching success, the length of the egg period, and the number of eggs laid than did harvesting all eggs from 20% of the nests (Fig 3). This held true whether the harvest was conducted on a single day (day 15) or spread over 5 or 10 days (beginning on day 15).

All harvest schedules significantly reduced hatching success from levels with no harvest ( $F = 30386$ ,  $df = 19$ ,  $P < 0.001$ ). Post-hoc analysis showed that harvesting from 2% of the nests for 10 consecutive days resulted in the greatest reduction of hatching success ( $P < 0.001$ ). Varying harvest schedules significantly influenced the length of the egg period ( $F = 169$ ,  $df = 19$ ,  $P < 0.001$ ). At very low predation rates, harvesting 2% for 10 consecutive days increased the mean length of the egg period most (to  $72.93 \pm 0.54$  days) whereas harvesting 20% on 1 day decreased the mean length of the egg period (to  $65.31 \pm 0.66$  days). Larger harvests on a single day forced replacement laying to be synchronous, which reduced the time needed for all nests to hatch. In contrast, smaller harvests over 10 days more closely resembled constant low predation and caused

asynchronous replacement laying, which increased the time needed for all nests to hatch or reach the replacement laying limit.

All harvest schedules increased the number of eggs laid by gulls from simulations with no harvest ( $F = 20665$ ,  $df = 19$ ,  $P < 0.001$ ). The differences were greatest when predation rates were very low. As predation rates increased, harvesting had less of an effect. The number of eggs harvested varied significantly with predation and harvest schedule ( $F = 7455$ ,  $df = 19$ ,  $P < 0.001$ ). However, harvesting from 2% of nests on 10 consecutive days resulted in more eggs collected regardless of the background predation level.

*Harvest date.*-- Varying the date on which a 20% harvest occurs affected hatching success ( $F = 35824$ ,  $df = 14$ ,  $P < 0.001$ ), the length of the egg period ( $F = 426$ ,  $df = 14$ ,  $P < 0.001$ ), the total number of eggs laid ( $F = 19591$ ,  $df = 14$ ,  $P < 0.001$ ), and the total number of eggs harvested ( $F = 197$ ,  $df = 14$ ,  $P < 0.001$ )(Fig 4). When a 20% harvest was conducted later in the season (on day 30), hatching success was significantly reduced regardless of background predation rates ( $P = 0.001$ ). Later harvests also increased the length of the egg period and the total number of eggs gulls laid, but only when background predation levels were low to moderate. At very high predation levels, there was less of an effect of harvest date on the length of the egg period. In fact, a late harvest decreased the total number of eggs laid by gulls. Harvesting later generally resulted in greater numbers of eggs collected. However, as background predation rates increased, fewer eggs were collected. This pattern of decline was greatest when harvests were conducted on day 30.

*Harvest amount.*-- Increasing the extent of a harvest on a single day (Fig. 5) had significant effects on hatching success ( $F = 37381$ ,  $df = 19$ ,  $P < 0.001$ ), the length of the egg period ( $F = 94$ ,  $df = 19$ ,  $P < 0.001$ ), the total number of eggs laid ( $F = 13944$ ,  $df = 19$ ,  $P < 0.001$ ), the total number of eggs harvested ( $F = 10180$ ,  $df = 19$ ,  $P < 0.001$ ), and the number of times predators encountered no nests with eggs ( $F = 553$ ,  $df = 19$ ,  $P < 0.001$ ; not illustrated). Increasing harvest levels decreased hatching success at all background predation levels. However, the effects of increasing harvests from 80 to 100% of the nests on a single day were not significantly different (Tukey's HSD  $P = 0.63$ ).

Doubling of single-day harvest amounts from 20% to 40% of nests had no significant effect on the length of the egg period (Tukey's HSD  $P = 0.16$ ). However, increasing harvests to 100% resulted in synchronous replacement laying, so the egg period ended earlier than when background predation was low. At mid to high levels of predation, increasing harvests from 20% to 100% had little or no effect on the length of the egg period.

At low levels of predation, gulls effectively replaced eggs that were harvested. For example, when predation rates were 0.001, harvesters collected 97-99 more eggs by harvesting from all nests rather than only 20%, and gulls laid 95-97 more eggs to replace those collected. When predation rates were 0.055, harvesters still collected 63-65 more eggs by harvesting from all the nests, but the gulls only laid an additional 15-17 eggs. When losing eggs to harvesters and predators at such high levels, more gulls reached their limit of replacement eggs, and hatching success was only 10%.

## **DISCUSSION**

We believe this model is a useful tool for exploring the variables that influence the fate of gull eggs on South Marble Island. The parameters in this model are realistic, based on fieldwork or published data. By designing and using this model, we were able to simulate scenarios that are otherwise impossible to study. We wanted to produce a model that was simple enough to understand, yet complex enough to simulate the interaction among gulls, eagles, and people. Accordingly, not all parameters are adjustable (clutch size) nor do all assumptions precisely mimic the real world (predation). We chose to test three harvest strategies, when in fact, eggs on South Marble Island are harvested in many ways (Hunn et al 2002).

The average daily predation rates we observed in reference nests in 1999 and 2000 are within the range where our model predicts modifying harvest strategies will produce different outcomes. Admittedly, averaging daily predation to constant values is a simplification of actual predation, in which the numbers of nests attacked fluctuates daily. However, predation events occurred throughout the egg period in both years, representing chronic, if not constant, predation. We would expect actual hatching success values to be lower than those predicted by the model because other factors that depress hatching success were not included in the model. For example, abnormal weather patterns have caused massive nest failures in ring-billed gulls (Brown and Morris 1996). Gulls have been documented eating or destroying eggs of conspecifics (Good et al 2000). A small proportion of eggs commonly fail to hatch in many gull species. In addition, not all glaucous-winged gulls lay full 3 egg clutches (Verbeek 1993, Zador 2001). Although eagles appeared to be the main cause of nest failure at the South Marble Island colony

during our study, eggs may have been lost due to these other factors, thereby decreasing actual hatching success.

The gulls in our simulations respond more negatively to chronic exposure to predation than to episodic predation (i.e. harvest). When daily predation rates are high, gulls do so poorly that harvesting makes little difference to hatching success, the length of the egg period, or the total numbers of eggs laid. Only when predation rates are relatively low does modifying harvest strategies have a significant impact on the gulls. Consequently, to produce a desired outcome for the gulls or the harvesters requires knowledge of the levels of background predation, which is not controlled by resource managers.

To evaluate the full effects of egg loss for gull populations, it is also important to look beyond hatching success. We stopped short of this in our study because it was focused on the effects of harvest on egg and chick production. However, we know that seabird populations are ultimately regulated by factors such as rates of adult and juvenile survivorship, production of young, and recruitment of juveniles into the breeding population (Newton 1998). The length of the egg period is also an important factor to consider because it reflects the timing of hatching. Studies have shown that hatching later or hatching from replacement eggs can have a negative impact on the survival of the gull fledglings. Great black-backed gull chicks that hatch from later-laid eggs have lower fledging success despite equivalent hatching success (Nager et al 2000). Black-headed gull chicks that hatch late begin breeding at an older age (Prevot-Julliard et al 2000). The total number of eggs that gulls are forced to lay is also an important variable to consider because studies have shown that there are negative costs to laying replacement eggs.

Adult black-headed gulls that lay an extra egg do not fledge as many chicks (Monaghan et al 1998). Herring gulls hatched from replacement clutches have been found to suffer higher post-fledging mortality (Nisbet and Drury 1972). In fact, female glaucous-winged gulls on South Marble island that have replaced clutches show suppressed stress responses, which may compromise their survival (Zador 2001). Thus, despite having little or no effect on hatching success, the ultimate productivity of a colony may still be compromised by predation and harvest patterns that extend the length of the egg period and increase the total numbers of eggs the gulls lay. In fact, some management programs have used the repeated removal of all eggs as a method to reduce gull populations (Ickes et al 1998).

## **MANAGEMENT IMPLICATIONS**

Any strategy for management of gull egg harvests needs to acknowledge the confounding effects of environmental variability and potential for post-hatching effects on chicks and adults that were not addressed in this study. Changes in food supply, predation pressure, or nesting space can be expected in a dynamic environment such as Glacier Bay, where rapid ecological succession follows glacial retreat (Crocker and Major 1955, Lawrence et al 1967).

Thus, we would recommend a conservative approach to egg harvest. To maximize the number of eggs collected while minimizing impacts on the gull colony on South Marble Island, we believe harvesters should restrict collections to one time, early in the season, and from no more than 20% of the nests in the colony. In effect, harvest strategies should be least similar to chronic predation. We encourage a regulated harvest because it allows

a controlled impact on the gulls. Huna harvesting traditions, as recently documented through oral histories, are varied (Hunn et al 2002). For example, recommendations to harvest early may seem intuitive, as eggs will be more developed if collected later in the season. However, some traditional users prefer these eggs (Hunn et al 2002). The effects of a controlled management plan can and should be evaluated regularly along with changes in the gull population, their nesting distributions, and predator pressures.

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Table 1. Results of simulations with the observed predation rates in reference nests in 1999 and 2000. N = 150 simulations with no harvest for each year.

	Observed	Predicted	Observed	Predicted
	1999		2000	
Predation rate	0.007		0.009	
Hatching success <sup>1</sup>	61 ± 5	83.62 ± 0.17	70 ± 4	75.24 ± 0.18
Eggs laid <sup>2</sup>	152	187 ± 0.24	187	202 ± 0.31
Egg period (days) <sup>3</sup>	55+	70.13 ± 0.32	78+	68.21 ± 0.29

<sup>1</sup> For the nests in 1999 and 2000, hatching success was calculated as the percentage of nests that hatched ≥ 1 chick. Nests with 1 or more eggs that had not yet hatched a chick when last checked were excluded.

<sup>2</sup> For comparative purposes, calculated by multiplying the mean number of eggs laid per nest in each year by 50.

<sup>3</sup> Nest observations ended before all eggs had hatched.

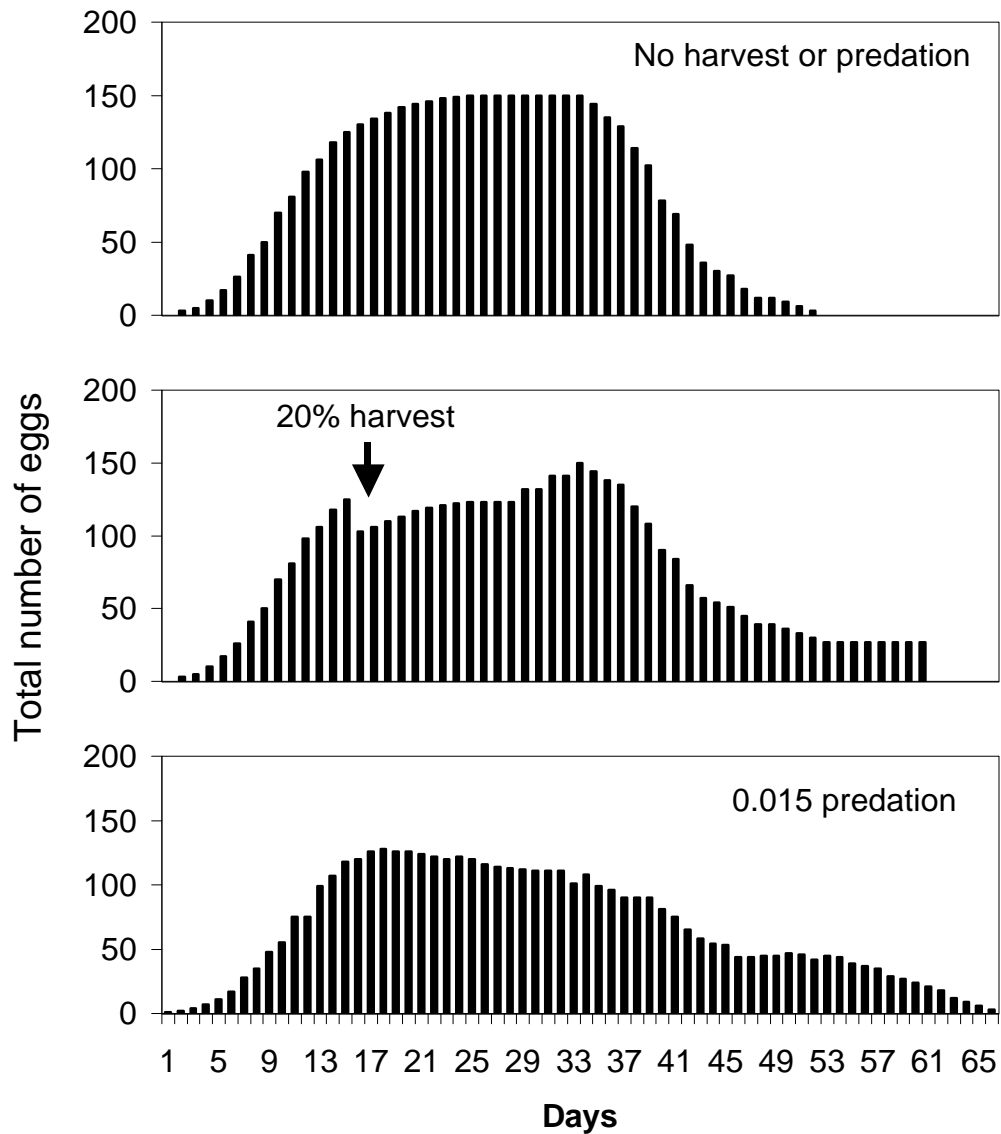


Figure 1. Example outputs of the egg harvest simulation model run once under three different scenarios. In all cases, the number of nests was set at 50. Histograms show the total number of eggs present in 50 nests each day after a single simulation run with no predation (top), with 20% of the nests harvested on day 15 (middle), and with a daily predation rate of 0.015 nests/day (bottom).

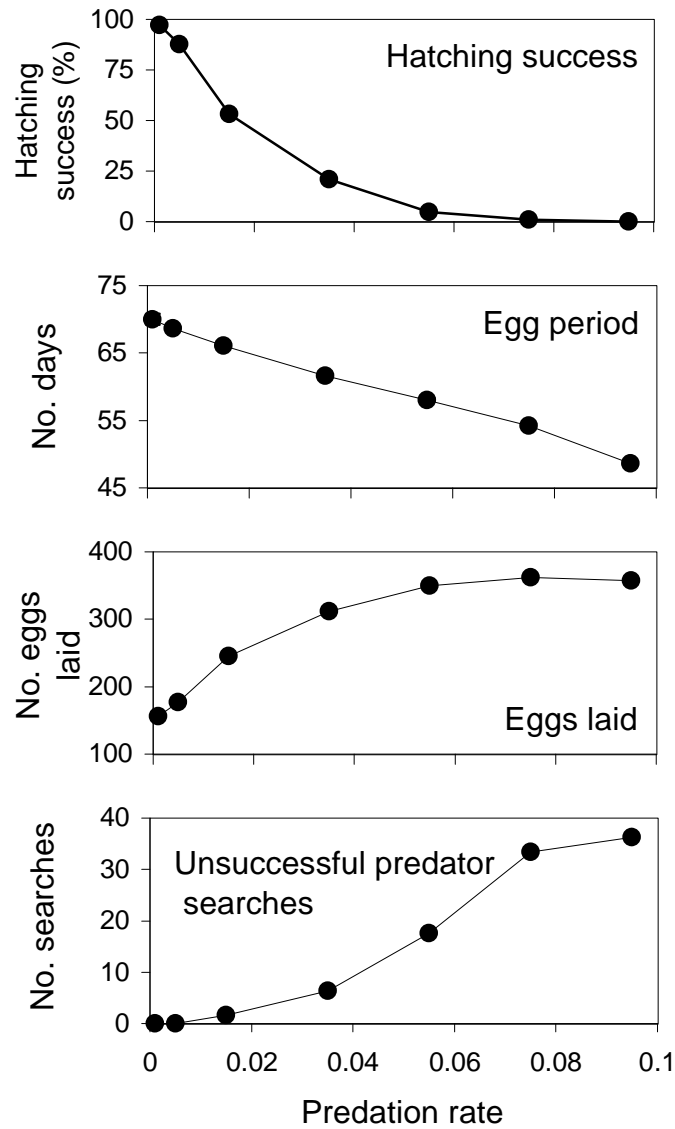


Figure 2. Effect of varying predation rates on hatching success, length of the egg period, total number of eggs laid, and number of unsuccessful predator searches. Values (+/- 1 SE) calculated as a function of varying daily predation rates (n = 150 simulations). Note that standards errors are so small that they are hidden by data points.

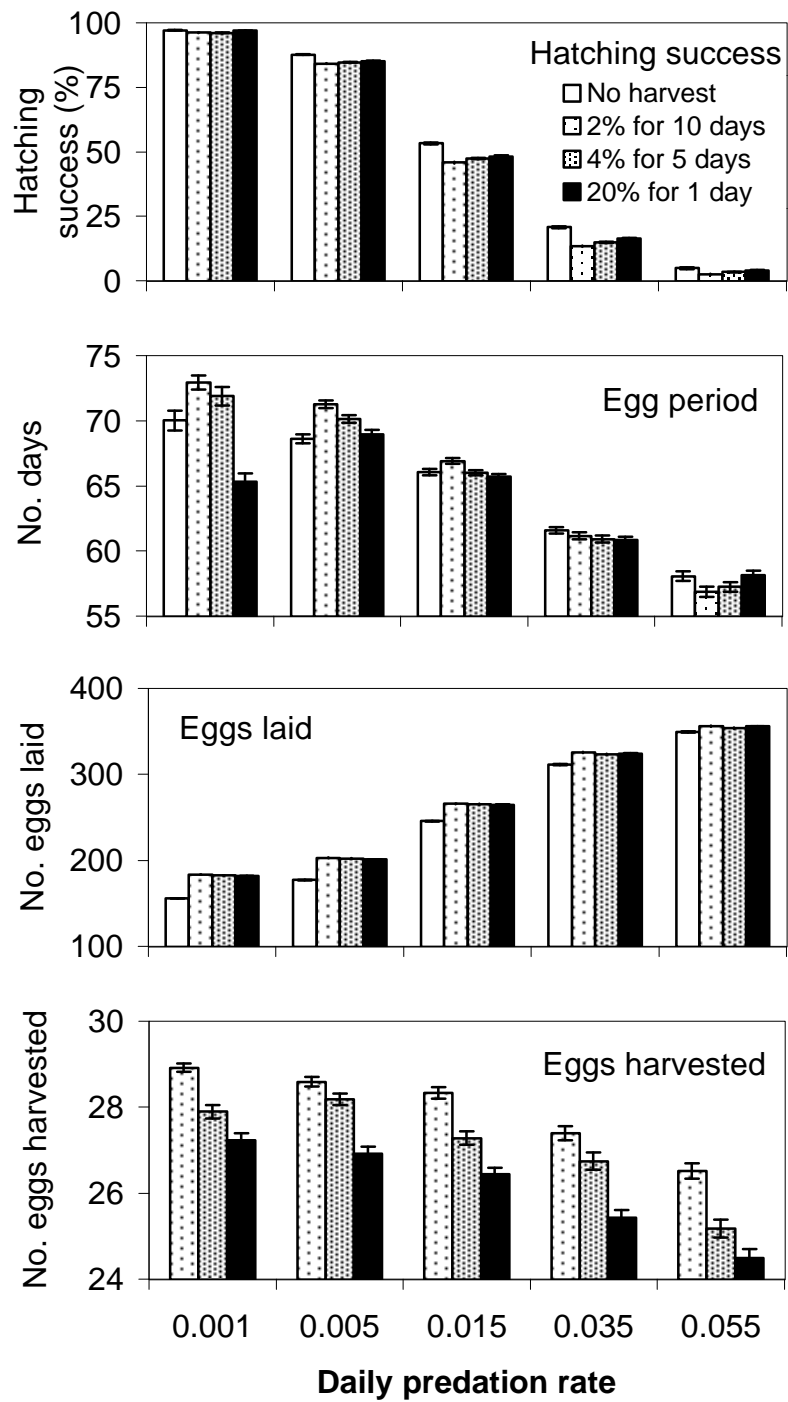


Figure 3. Effects of varying predation and harvest schedule on hatching success, the length of the egg period, the total number of eggs laid, and the number of eggs harvested. N = 150 model simulations of 50 nests.

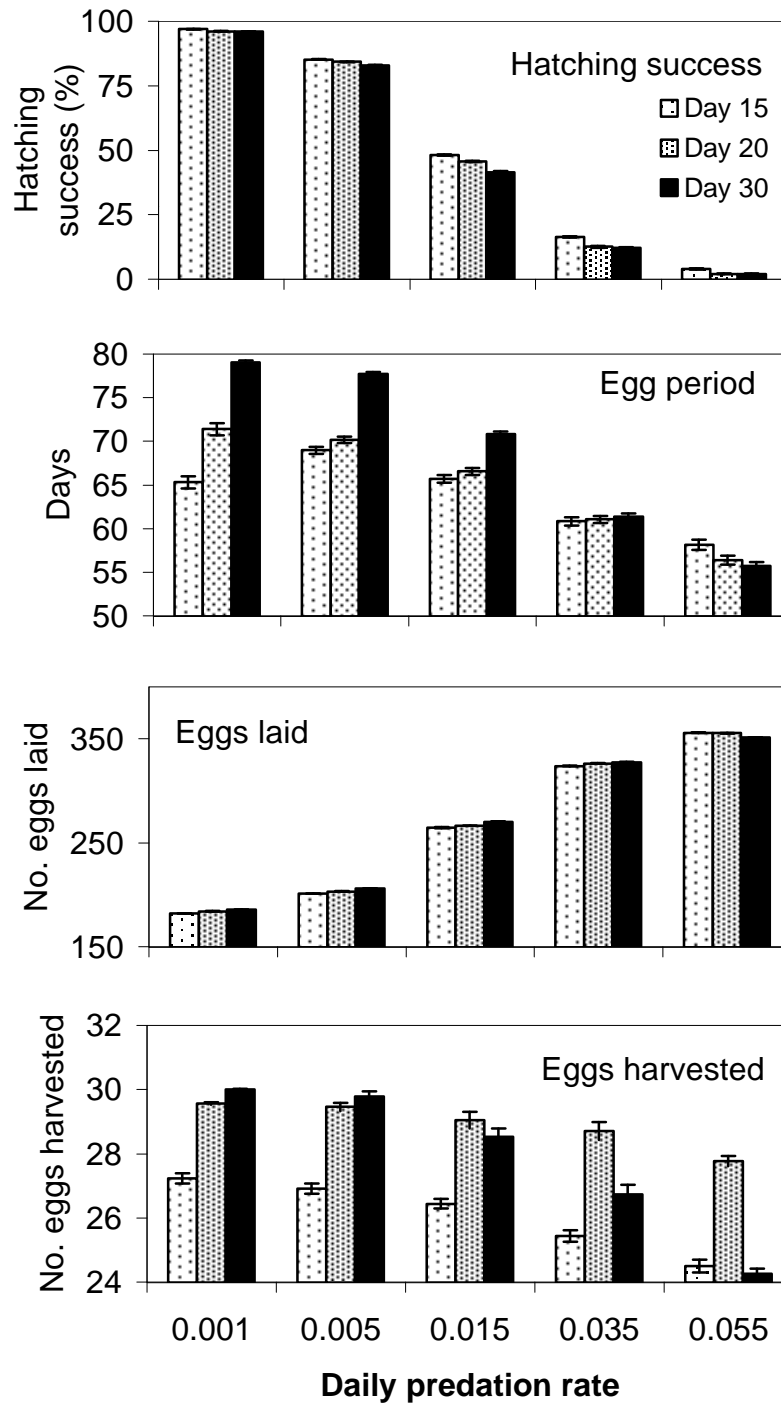


Figure 4. Effects of varying the timing of harvest on hatching success, the length of the egg period, the total number of eggs laid, and the number of eggs harvested. N = 150 simulations of 50 nests.

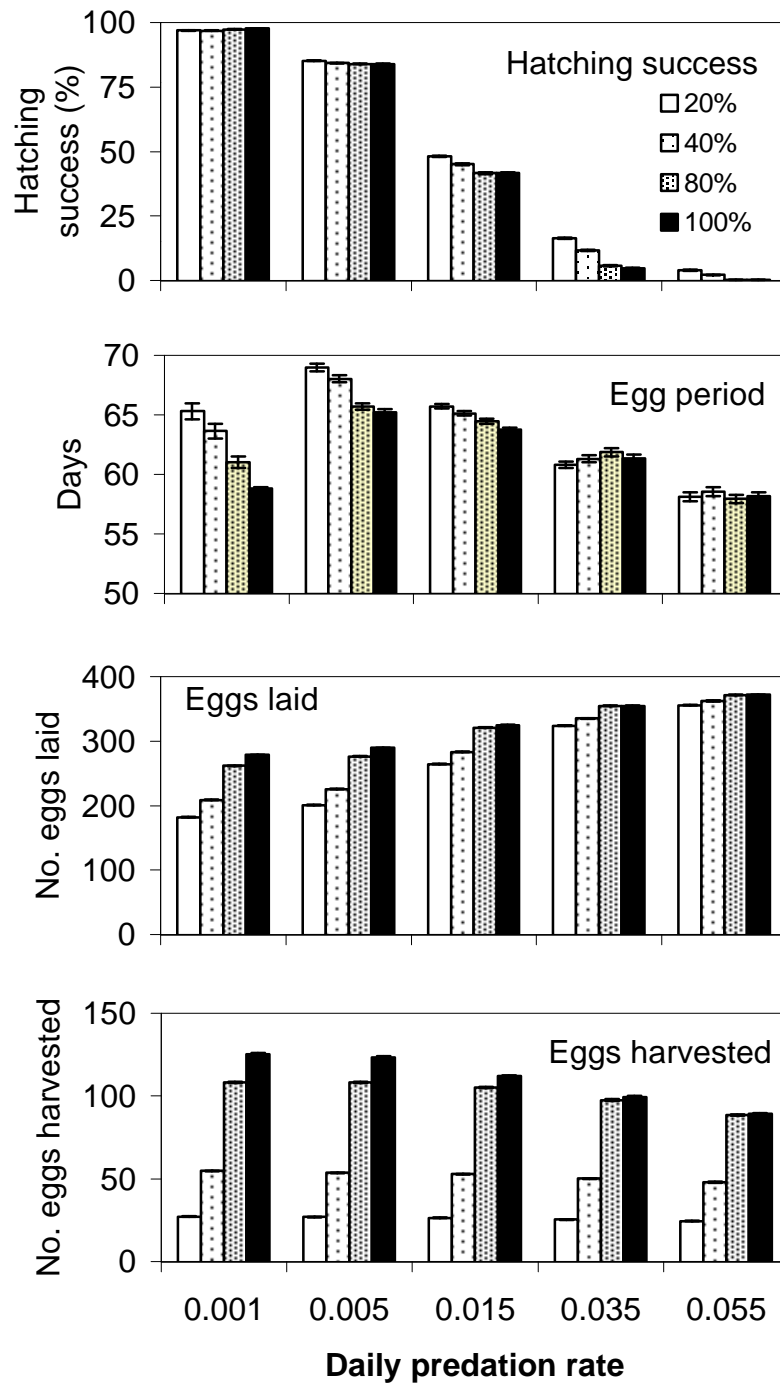


Figure 5. Effects of varying the number of nests from which eggs were harvested on a single day (day 15) on hatching success, the length of the egg period, the total number of eggs laid, and the number of eggs harvested. N = 150 model simulations of 50 nests.