Strategic nest attendance by Great Egrets

The Ecology of Parental Wisdom

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When young egrets reach three to four weeks of age, parents must weigh competing challenges of guarding the nest against predators and gathering food from surrounding wetlands.

I once watched a pair of ravens land next to a Great Egret nest that was occupied by two unguarded chicks. Immediately, the ravens proceeded to harass the young birds. After dodging several bill-thrusts from the defensive egret chicks, one of the ravens grabbed a nestling by its bill, pulled it down, and killed it. Although events like this seem gruesome, they are not unusual in heronries. Chicks guarded by adults are virtually immune to attack by ravens, but, surprisingly, herons and egrets typically leave their young unattended at the nest. We are currently working to understand this paradox, by investigating just how Great Egrets *(Ardea alba)* nesting at ACR's Bolinas Lagoon Preserve schedule their nest attendance duties to maximize their ability to fledge healthy young (Rothenbach and Kelly, in preparation).

Midway through the nesting cycle, herons and egrets shift from "guardian" to "post-guardian" nest attendance behavior. During the guardian period, parents share incubation duties by alternating their time at the nest so that, together, they attend the nest continuously. After the eggs hatch, adults continue to take turns attending the nest and foraging. When one parent arrives at the nest with food for the nestlings, the other takes off to search for more food. When Great Egret nestlings reach three to four weeks of age, both parents begin to forage for food simultaneously. This combined feeding effort provides young with more food but leaves them unguarded except during brief, frenzied feeding episodes. As nestlings grow, they become more defensive and the likelihood of nest predation declines, but younger, smaller nestlings can be easily taken by predators. Presumably, the intensified, post-guardian feeding activity gives fledglings a valuable head start. But how much time should parents devote to finding food vs. guarding their young?

The care of parents for their young is common throughout nature, sometimes revealing impressive or even heroic efforts. What interests ecologists is that such care is generally adaptive and often strategic. In birds, patterns of nest attendance are strongly influenced by the developmental needs of their eggs and nestlings, by the challenges of finding enough food to support a family, and by the complex and dynamic behaviors of nest predators. A complete commitment to any one of these concerns, however, can result in the neglect of other needs. So how do egrets determine the best way to manage family responsibilities? As in humans, the best egret parenting is ad hoc and depends on an ability to make wise decisions in response to changing conditions.

How parents make decisions

To examine nest attendance choices, we addressed two hypotheses based on numerous observations of Great Egret nests subject to the risk of predation by resident Common Ravens *(Corvus corax)*. First, we considered the "Trade-off Hypothesis"—that egrets guard their nests continuously, to reduce predation risk, until increasing food demand of the developing nestlings forces both parents to forage for food simultaneously. This idea proposes that the increasing risk of nestling starvation forces parents to leave their nests unguarded. To test this hypothesis, we evaluated how the age of chicks at the onset of the post-guardian period affects reproductive performance.

Under the Trade-off Hypothesis, we predicted that egrets would guard their nests as long as possible and that fewer nests therefore would be taken by predators. We expected that the associated sacrifice of foraging time might reduce the number of chicks produced in successful nests, because some of the young might starve. Among

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As nesting egrets grow large, both parents work to meet the increased food demand, returning to the nest only for frenzied feeding visits.

nests that successfully avoid predation, however, those with shorter guardian periods should be able to raise more young. We also expected a narrow range of chick ages at the onset of the post-guardian period, because parents might guard their nests until their young reach some critical age when food demand forces both parents to search for food. Finally, under the Trade-off Hypothesis, we expected relatively little synchrony in the onset of post-guardian behavior in the colony, because nests initiated at different times should reach the critical nestling age at different times.

Second, we tested the "Dilution Hypothesis"—that adult egrets in a colony synchronize the time of the season when they begin to leave their nests unguarded, to reduce the per capita risk of predation by spreading risk across a larger pool of vulnerable nests. Nestlings are more likely to be taken by predators when they are smaller, so the most dangerous time of the season is when the developing young are first left unattended. To test Dilution Hypothesis, we counted the number of other post-guardian nests in the colony on the day when each nest was first left unattended.

Under the Dilution Hypothesis, we predicted that, in each successful nest, more chicks would be fledged: if reduced per capita risk of nest predation allows parents to focus more time on foraging for food, they may be able to support larger families. We also expected that greater synchrony in leaving nestlings unattended might lead to more nest failures, because any late broods, with relatively small chicks, might be easily taken by predators. Finally, under the Dilution Hypothesis, we expected a wider range of chick ages at the onset of the post-guardian period, a necessary result of synchronizing parental behavior among nests initiated at different times.

Measuring parental behavior

The nesting performance of all breeding pairs of egrets in the heronry has been monitored annually since 1967 (Pratt and Winkler 1985, Kelly et al 2007). For this study, we used nesting data from 19 years (1984,1987–1997, and 2002–2008), excluding years when there was no observed nest predation or when the timing of the post-guardian period was not precisely measured.

To focus on the parents' competing challenges of finding food for nestlings and protecting them from predators, we included nests only if they met the following criteria: (1) at least one egg was hatched; (2) nest failure, if it occurred, was caused by predation; (3) the length of the guardian period was precisely determined; and (4) the nest was the first of the season at that nest site and likely to have been the parents' first attempt that season (initiated before colony size began to decline). If an entire brood disappeared between observations, we assumed that it was taken by a predator.

To account for differences in parental behavior between successful and unsuccessful nests, and among successful nests that fledged one, two, or three young, we compared several statistical models (explanations of egret behavior) based on observations of nesting egrets. The models included controls to account for annual differences in colony productivity, intra-seasonal timing, and environmental factors such as rainfall or temperature. The analysis also distinguished egret parental behavior between years with and without resident

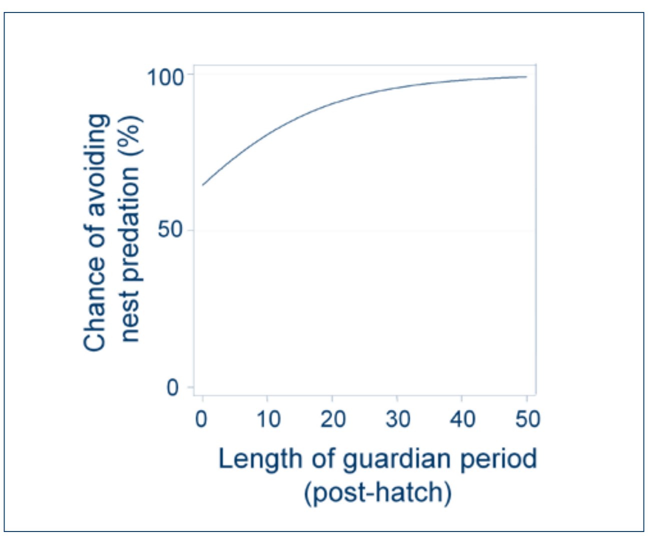

Figure 1. Average percent of Great Egret nests that escape predation in relation to the length of the nest guardian period (days after first hatch).

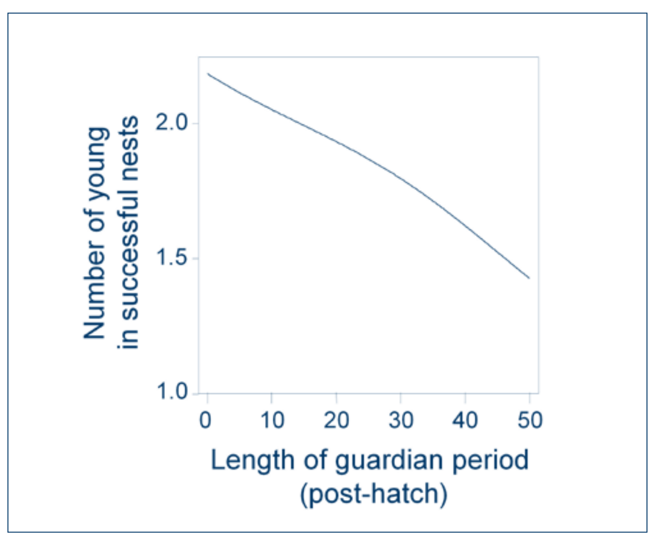

Figure 2. Great Egret parents with successful nests (not taken by predators) are likely to fledge more young if they reduce the length of the nest guardian period.

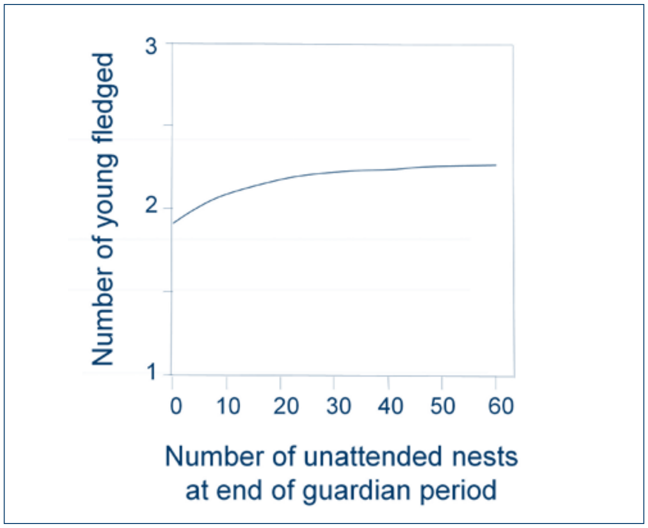

Figure 3. Great Egrets fledge more young, on average, if parents begin the post-guardian period of nest attendance at a time when more nests in the colony are unattended.

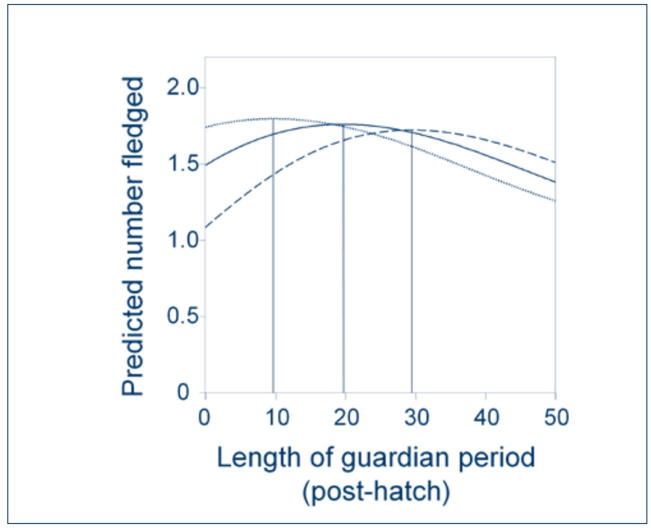

Figure 4. Predicted number of Great Egrets fledged per nest attempt at Bolinas Lagoon, plotted against the length of the nest guardian period (at average values of other variables). Dashed line = ravens present; dotted line = ravens absent; solid line = 50% chance of raven presence. Vertical reference lines indicate the predicted length of the guardian period.

ravens. We then examined the extent to which the consequences of parental behavior explained by the models were consistent with the predicted outcomes of the Dilution and Trade-off hypotheses.

Patterns of parental care

Our results were consistent with the predictions of the Trade-off Hypothesis. When egrets guarded their nests for a longer period of time, they decreased the chance of nest predation (Figure 1). However, parents that successfully avoided nest predation were likely to fledge more young if they reduced the length of the guardian period (Figure 2)—presumably because of increased time for foraging. We also found support for the Dilution Hypothesis. Great Egrets fledged more young, on average, if they began the post-guardian period when more unattended (post-guardian) nests were present in the colony (Figure 3).

Egrets that made complex decisions to optimize trade-offs in reproductive performance related to the combined risks of nest predation and nestling starvation—decisions influenced by the age of nestlings, energy demand, food supply, foraging opportunities, and predation pressure—achieved the highest reproductive success (Figure 4). How sensitive are nesting egrets to changes in predation risk and opportunities for foraging? Simulations based on our results suggested that egrets are likely respond to increases in the presence of ravens by extending the length of the guardian period, which reduces available foraging time (Figure 4). Under simulated decreases in the presence of ravens, egrets reduced the length of the guardian period, increasing foraging time.

Conservation trade-offs

Successful parenting involves complex choices based on continual assessments of multiple concerns. The most successful Great Egret parents balance the costs and benefits of guarding the nest continuously, leaving to gather food for their young, and aligning the peak period of nest vulnerability with other nests in the colony. These costs and benefits have potentially important implications for conservation.

Based on our results, restoring the quality or quantity of surrounding wetland feeding areas might not only allow nesting egrets to reduce their foraging range, spend less time foraging, or increase the amount of food they bring back to their young—it may also allow parents to increase the length of the nest guardian period. This, in turn, might allow them to compensate for increases in predation pressure related to introduced nest predators or human subsidies of ravens or other predators. Similarly, reducing the threats of introduced or subsidized nest predators in heronries might allow egret parents to reduce the length of the nest guardian period, increasing the amount of time they can spend gathering food for their young. This, in turn, would reduce the risk of nestling starvation and help parents compensate for reduced wetland quality or quantity, including wetland losses related to climate-induced sea level rise.

If conservation efforts can protect or improve heron and egret foraging opportunities in surrounding wetlands and can limit or reduce threats caused by introduced or subsidized nest predators, then herons and egrets might be able to sustain effective levels of reproduction through adaptive parenting—in spite of dramatic changes to the environment. Alternatively, the expected result of spiraling demands on egret parents is declining colony size or abandonment of the colony site. As in other areas of conservation, the ecological implications of nesting behavior suggest benefits and concerns for the protection of heronries.

References cited

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