THE PARENTAL DILEMMA UNDER VARIABLE PREDATION PRESSURE: ADAPTIVE VARIATION IN NEST ATTENDANCE BY GREAT EGRETS

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Abstract. Birds' choices concerning nest attendance are influenced by state-dependent and environmental variables including food availability and predation pressure. Parents of altricial young with biparental care face a dilemma: they can choose to guard their nestlings against predation with their physical presence at the nest and ensure the fledging of at least one chick, or they can choose to leave the young unguarded so they can forage for more food, increasing provisioning rates and the probability of fledging more young. In group-nesting birds, parents may be able to dilute the risk of nest predation while leaving the nest to forage if they leave the nest unguarded when there are many other unguarded nests in the colony. The complexity of the parental decision to leave a nest unguarded is highlighted by variation in the chicks' age, within a nest and within the colony, and by differences in effects on nest success and nest fecundity. Our results suggest that the incremental fitness advantage of reducing predation risk by continuing to guard the nest is eventually outweighed by opportunities to reduce nestlings' risk of starvation. The effect is likely to reduce fledgling production within a colony when less food is available, which reinforces the importance of healthy and productive wetland ecosystems in maintaining viable populations of the Great Egret.

Key words: brood-guarding, Great Egret, nest attendance, nest predation, parental dilemma, predation-risk dilution, starvation trade-off.

El Dilema Parental bajo Presión de Depredación Variable: Variación Adaptativa en Asistencia al Nido por Ardea alba

Resumen. Las elecciones de las aves relacionadas a la asistencia al nido están influenciadas por variables ambientales, incluyendo la disponibilidad de alimentos y la presión de depredación. Los padres de jóvenes altriciales con cuidado biparental enfrentan un dilema: pueden elegir proteger sus pichones de la depredación con su presencia física en el nido y asegurar el emplumamiento de al menos un pichón, o pueden elegir dejar al polluelo desprotegido, de modo que pueden ir en busca de más alimentos, incrementando las tasas de aprovisionamiento y la probabilidad de criar más jóvenes. En aves que anidan en grupo, los progenitores pueden ser capaces de diluir el riesgo de depredación del nido mientras dejan el nido para forrajear si dejan el nido desprotegido cuando hay muchos otros nidos desprotegidos en la colonia. La complejidad de la decisión parental de dejar un nido desprotegido se agudiza con relación a la variación en la edad del pichón, dentro del nido y de la colonia, y por diferencias en los efectos sobre el éxito y la fecundidad del nido. Nuestros resultados sugieren que la ventaja incremental en la adecuación biológica dada por la reducción del riesgo de depredación mediante la vigilancia continua del nido es eventualmente compensada por las oportunidades de reducir el riego de hambruna del pichón. El efecto probablemente reduce la producción de pichones dentro de la colonia cuando hay disponible una menor cantidad de alimentos, lo que refuerza la importancia de ecosistemas de humedades saludables y productivos para mantener poblaciones viables de *Ardea alba*.

INTRODUCTION

Nest-attendance choices by birds are influenced by state-dependent variables, such as parental condition and nestling development (Houston and McNamara 1999, Whittam and Leonard 2000), and environmental variables, including weather or thermal conditions (Bancroft et al. 1988, Witt 2006, Catry et al. 2010), food availability (Dewey and Kennedy 2001), and predation pressure (Furness and Monaghan 1987, Thompson and Raveling 1987, Clutton-Brock 1991). In altricial birds with biparental care, parents are confronted with a behavioral dilemma that involves a trade-off between maintaining a continuous presence at the nest to minimize the risk of nest predation and lowering the risk of nestling starvation by leaving the nest unguarded to forage for food (Regehr and Montevecchi 1997, Dewey and Kennedy 2001, Catry et al. 2006b). When food availability declines or nestlings' demand for food increases, adults must forage longer to adequately provision their brood. If parents satisfy this demand by foraging simultaneously for food, the brood is subject to increased risk of predation. Alternatively, if parents continue guarding the nest at the expense of additional foraging time, nestlings

are subject to increased risk of starvation. Nesting birds that optimize these risks are likely to maximize their reproductive performance. In colonially nesting birds, individuals may be able to further reduce the per capita risk of nest predation, or the associated risk of nestling starvation, by aligning the intraseasonal timing of nest initiation and nest attendance during the postguardian period (first extended absence of both adults) with nearby nesting pairs (Foster and Treherne 1981, Findlay and Cooke 1982, Catry et al. 2009).

Each spring, Great Egrets (*Ardea alba*) form nesting colonies that may include Great Blue Herons (*A. herodias*), Snowy Egrets (*Egretta thula*), or other Ardeidae. Large platform nests are placed high in trees and are usually exposed from above. One to six eggs (usually three) are laid and incubated for 25–29 days before chicks hatch (Pratt 1970, Pratt and Winkler 1985, McCrimmon et al. 2001). Because incubation begins with the first or second egg, hatching is asynchronous. This creates an age-related size hierarchy among nestlings that affects their ability to compete for food, leading to differential survival and brood-size reduction in most nests. After the eggs hatch, adults take turns guarding the nest and foraging for food for 12–40 days before the chicks are left unguarded for the first time (Kushlan and Hancock 2005). Young Great Egrets are able to fly at 7 weeks of age but generally remain in or near the nest for 7 to 10 weeks or longer (Pratt and Winkler 1985, McCrimmon et al. 2001).

As the nestlings grow older, the guardian nest-attendance behavior of parents gives way to postguardian behavior when parents leave nestlings unattended (Voisin 1991). During the postguardian period, parents are able to enhance their ability to provision nestlings by foraging simultaneously (Mock et al. 1987, Sullivan 1988). Variation in the length of the nest-guardian period among nests in a colony is substantial and well known (Milstein et al. 1970, Pratt 1970, Catry et al. 2010). Long-term monitoring of Great Egret nests at the Martin Griffin Preserve of Audubon Canyon Ranch, near San Francisco, California, revealed that the duration of the guardian period after the hatching of the first egg was 22.0 ± 6.6 days (SD; maximum 46 days, *n* = 1224 nests, 1967–2008; Audubon Canyon Ranch, unpubl. data). However, the adaptive value of such variation in nest attendance has not been widely investigated for altricial birds (Varpe et al. 2004, Catry et al. 2009) and has not been studied in the Great Egret.

To investigate adaptive variation in the timing of postguardian nesting behavior, from 1984 to 2008 we evaluated Great Egret behaviors at nests subject to predation. We tested two non-exclusive hypotheses regarding adaptive variation in nest attendance in relation to the competing risks of nest predation and nestling starvation. First, we tested the *starvation trade-off hypothesis*, that parents should shift from guardian to postguardian nest attendance when nestlings reach an age that corresponds to a decline in the parents' potential fitness, related to nestlings' increasing risk of starvation (age-related

food demand) relative to the declining risk of nest predation (age-related nestling vulnerability; Varpe et al. 2004; the "chick-protection hypothesis" of Catry et al. 2009). Accordingly, nesting egrets should have greater reproductive success if they extend or shorten the period they continuously guard their nests in response to increases or decreases, respectively, in nest-predation pressure. Second, we tested the *predation-risk dilution hypothesis* that egrets shift from guardian to postguardian nest attendance when the increasing number of unattended nests in the colony dilutes the per capita risk of nest predation to a level that corresponds to an increase in potential fitness if parents begin to forage simultaneously to meet nestlings' increasing food demand (Darling 1938, Ims 1990; the "synchronization hypothesis" of Catry et al. 2009). Accordingly, nesting egrets should have greater reproductive success if they shift to postguardian nest attendance when a substantial number other nests are left unattended. Together, these hypotheses predict that nesting egrets should optimize nest-guardian behavior with regard to nestling age and number of postguardian nests in the colony, guarding nests continuously until potential fitness begins to decline, then leaving the nest unattended to forage simultaneously for food. Other influences may be involved, such as variation in energy reserves of adults when nesting begins, breeding experience of parents, brood size, or nutritional states of offspring (Houston and McNamara 1999). We used the resulting models to predict variation in nest-guardian behavior in relation to differences in predation pressure. We measured fitness values on the basis of successful vs. unsuccessful nests and the number of young produced in successful nests.

METHODS

The Martin Griffin Preserve of Audubon Canyon Ranch is adjacent to Bolinas Lagoon along the Pacific coast of California, approximately 50 km north of San Francisco. The preserve hosts a mixed nesting colony of Great Egrets, Great Blue Herons, and Snowy Egrets. The nesting performance of all breeding pairs in the heronry has been monitored annually since 1967 (Pratt and Winkler 1985, Kelly et al. 2006). Each year, between 49 and 150 Great Egret nests are initiated in the colony at the Martin Griffin Preserve. In this study, we used 19 years of data on Great Egret nesting (1984,1987–1997, and 2002–2008), excluding years that (1) had fewer than five confirmed cases of predation (to achieve minimum sampling requirements; Hosmer and Lemeshow 1989), (2) included catastrophic interference by predatory raccoons (*Procyon lotor*), or (3) were based on observations that could not be used to determine the precise length of the nest-guardian period. Nest predation during the years selected was primarily by Common Ravens (*Corvus corax*); resident ravens have occupied the vicinity of the heronry continuously since 1993

(Kelly et al. 2005). Nests that are depredated by ravens usually, though not always, fail entirely. However, nest predation by ravens rarely occurs if an adult Great Egret is at the nest, and unattended chicks gain competence in repelling ravens as they grow.

We included a nest (n = 1132) in the analysis only if it met the following criteria: (1) at least one egg hatched; (2) nest failure after hatching resulted from predation; (3) the number of days from first hatching to the onset of the postguardian period could be determined; (4) it was a first nesting attempt at that nest site that year; (5) the nest was initiated before colony size began to decline (to avoid second nesting attempts). We assumed that nest failure was caused by predation if the entire brood disappeared between observations or if the partial remains of nestlings were observed in the nest. To determine whether nests were successful and how many young were fledged from successful nests, we monitored all nests at least once every 2–4 days, from nest building until all young departed from the nest. We assumed a nest was successful if nestlings reached the minimum fledging age of 49 days, the age when young egrets are old enough to fly across open space to locations away from the nest site (Pratt and Winkler 1985).

Under the starvation trade-off hypothesis, we expected nest survivorship to increase with the length of the guardian period (nestling age) because older nestlings are more proficient at deterring predators (Table 1). Therefore, we expected younger nestlings to be left unattended in years of low predation risk and older chicks to be left unattended in years of high predation risk. In contrast, the number of young produced in *successful* nests should decline with chick age because of constraints on adults' foraging time imposed by longer periods of continuous nest attendance (increased starvation risk). Together, these predictions suggest optimum timing for shifts in nest-guardian behavior with regard to overall reproductive success, when the parental benefits of foraging simultaneously to meet nestlings' increasing food demand outweigh the declining importance of continuous nest attendance to deter predators (Table 1).

If the predation-risk dilution hypothesis is supported, egrets should shift to postguardian nest attendance when the number of postguardian (unattended) nests in the colony increases, reducing the per capita risk of nest predation (after development of homeothermy; age >7 days; McCrimmon et al. 2001). Therefore, under this hypothesis, we expected greater nest survivorship among egrets that shift to postguardian nest attendance when there are more unattended nests in the colony (Table 1). In contrast, we expected the number of unattended nests in the colony to have no effect on the mean productivity of successful nests: although egrets initiating nests relatively late in the season might shorten the guardian period if predation risk is shared with many other unattended nests, any increases in the time available for provisioning chicks may be balanced by greater brood reduction (starvation) in earlier nests guarded for longer periods of time to avoid higher per capita risks of nest predation. On average, however, we expected an increase in overall reproductive success if parents synchronously shift to postguardian behavior, reducing the per capita risk of nest predation and increasing opportunities to forage simultaneously for food (Table 1).

STATISTICAL ANALYSIS

We used logistic regression (Hosmer and Lemeshow 2000) and an information-theoretic approach (Burnham and Anderson 2002) to evaluate factors affecting the Great Egret's behavioral shift from guardian to postguardian nest attendance. We constructed two sets of models based on outcome variables for (1) successful nests vs. unsuccessful nests and (2) successful nests fledging one, two, or three young. Independent predictor variables (Table 2) were identical in both sets of models and included (1) the age of the oldest nestling at onset of the postguardian period (Age); (2) the number of other nests in the colony that had reached the postguardian period when each nest was first left unattended (Nests); (3) intraseasonal timing, measured as the Julian date of the first evidence of egg laying (Egg date, included in all models); (4) predation pressure, measured as a bivariate variable for the

TABLE 1. Predicted consequences of the shift by Great Egrets from guardian to postguardian behavior, with regard to nestling age and number of unattended nests in the colony (indicators of adaptive response for starvation trade-off and predation-risk dilution hypotheses) at the end of the nest-guardian period.

	Nestling age (starvation trade-off hypothesis)	Number of unattended nests in the colony (predation-risk dilution hypothesis)
Nest survivorship	+	+
Number of young produced in successful nests	—	no change
Overall reproductive success (mean productivity across all nest attempts)	increase to optimum, then decline	+

TABLE 2. Means (± SE) of the age of the oldest nestling (Age), the number of other postguardian nests in the colony (Nests), the Julian date of nest initiation (appearance of the first egg, Egg date), and the presence/absence of ravens (CORA) at the initiation of postguardian nest attendance, for failed nests and nests that successfully fledged 1, 2, or 3 young at Bolinas Lagoon, California, 1984–2008.

Variable	Failed ($n = 196$)	Successful ($n = 936$)	Fledged 1 ($n = 181$)	Fledged 2 ($n = 642$)	Fledged 3 ($n = 112$)
Age	18.5 ± 0.5	22.8 ± 0.2	23.8 ± 0.6	22.7 ± 0.3	21.3 ± 0.4
Nests	7.6 ± 0.6	11.1 ± 0.2	10.2 ± 0.6	11.2 ± 0.3	12.3 ± 0.7
CORA	0.9 ± 0.02	0.6 ± 0.02	0.6 ± 0.04	0.6 ± 0.02	0.5 ± 0.05
Egg date	116.8 ± 1.3	105.9 ± 0.5	110.3 ± 1.3	105.2 ± 0.5	102.9 ± 0.9

continuous presence or absence of resident (nesting) ravens in the immediate vicinity of the heronry (CORA; included in all models); (5) a categorical variable for year (Year; included in all models) to control for unmeasured annual variation in nest behavior related to differences in predation pressure, food availability, or other environmental factors such as rainfall or temperature (Maddock and Baxter 1991).

We developed eight a priori models within each set, based on hypothesized influences on nest-attendance choices, published information on the influences of intraseasonal timing and predation pressure on reproductive success and nesting behavior (Furness and Monaghan 1987, Thompson and Raveling 1987, Whittam and Leonard 2000, Dewey and Kennedy 2001), and our previous experience with nesting herons and egrets (Kelly et al. 2007, 2008; Table 3). The model sets differed only in the dependent variable used to evaluate the adaptive value of nest-attendance choices. Thus the two sets included identical a priori combinations of predictors and, together, accounted for key aspects of fitness: nest survivorship and the number of young produced in successful nests (Kelly et al. 2007). We used Akaike's information criterion, adjusted for small sample sizes (AIC$_c$; Akaike 1973, Hurvich

and Tsai 1989) to choose the best-supported model in each set, given the data (Burnham and Anderson 2002).

To address the starvation trade-off hypothesis, we tested predictions that reproductive success is affected by nestling age at the onset of postguardian behavior (Age), alone or with interacting effects of either intraseasonal timing (Egg date) or predation pressure (CORA; models 1, 5, and 6; Table 3). To address the predation-risk dilution hypothesis, we tested predictions that reproductive success is affected by the number of postguardian (unattended) nests in the colony (Nests), alone or with the interacting effects of Egg date or CORA (models 2, 7, and 8; Table 3). Finally, we tested predictions that Great Egrets' nest attendance is structured by both Age and Nests, with and without interacting effects (models 3 and 4; Table 3).

We centered all independent variables to reduce potential multicollinearity and aid in interpretation of the coefficients (Garson 2010). We examined residuals to confirm that the assumption of linearity in the logit held for each independent variable in the logistic regressions and tested each model for goodness of fit (Hosmer and Lemeshow 1989, Fagerland et al. 2008). Our data did not meet the parallel-lines (independence) assumption of ordinal logistic regression needed to compare nests with one young to those with two or more young and those with three young. Therefore, we used generalized ordinal logistic regression (procedures gologit and gologit2 in Stata; Williams 2006), which allows estimated coefficients of the ordinal contrasts of categories of the dependent variable to differ. To correct for nonlinearity in the logit of interaction terms, we used the Stata "inteff" procedure (Norton et al. 2004). However, the inteff correction does not exist for generalized ordinal logistic regression models (E. Norton and R. Williams, pers. comm.). Therefore, after running each generalized ordinal model, we ran the inteff correction for each binary logit regression within the model.

In each set of models, we evaluated the predictive ability of variables by calculating their model-averaged coefficients as follows: we multiplied the coefficient of each variable by the corresponding Akaike weight (w_i) of models in which it occurred, summed the products across all models, and divided the result by the sum of Akaike weights of

TABLE 3. A priori models used to evaluate factors affecting Great Egret nest success and the number of young produced in successful nests at Bolinas Lagoon, 1984–2008. See Table 2 for definitions of variables.

Independent variable	Model							
	1	2	3	4	5	6	7	8
Age	×		×	×	×	×		
Nests		×	×	×			×	×
Age × CORA						×		
Nests × CORA								×
Age × Egg date					×			
Nests × Egg date							×	
Age × Nests				×				
CORA	×	×	×	×	×	×	×	×
Egg date	×	×	×	×	×	×	×	×

all models in which the variable occurred. Confidence intervals calculated for each variable incorporated model uncertainty (Burnham and Anderson 2002). We then evaluated the degree to which model-averaged predictions and patterns of reproductive success were consistent with the predicted outcomes of the starvation trade-off and predation-risk dilution hypotheses (Table 1).

We evaluated the effects of nest-attendance patterns on overall reproductive success (number of young fledged per nest attempt) by combining the averaged models for nest survivorship and the number of young produced in successful nests into a single predictive model. We calculated predictive equations by using model-averaged coefficients that incorporated values of zero for models in which they did not occur (Burnham and Anderson 2002:152). Predictions for overall reproductive success were calculated as the product of estimated nest survivorship $\hat{s}$ and estimated number of young in successful nests $\hat{n}$:

$$\widehat{rs} = \hat{s} \cdot \hat{n}, \qquad (1)$$

where $\hat{s}$ is the conditional probability of nest success, $\pi_1(x)$, taken from the logistic regression of successful vs. unsuccessful nests, and $\hat{n}$ is the estimated number of young fledged from successful nests, calculated as

$$\hat{n} = \hat{p}(n_1) + 2\hat{p}(n_2) + 3\hat{p}(n_3),$$

where $\hat{p}(n_i)$ he estimated conditional probability of a nest producing one, two, or three young. These probabilities were derived from separate logistic regression (binary) contrasts between nests producing two or more young, $\pi_2(x)$, vs. only one young, and nests producing three young, $\pi_3(x)$, vs. less than three young:

$$\hat{p}(n_1) = 1 - \pi_2(x)$$
$$\hat{p}(n_2) = \pi_2(x) - \pi_3(x)$$
$$\hat{p}(n_3) = \pi_3(x).$$

Thus, overall reproductive success was calculated as

$$rs = \pi_1(x) \cdot \left\{ \left[1 - \pi_2(x) \right] + 2\left[\pi_2(x) - \pi_3(x) \right] + 3\pi_3(x) \right\} \quad (2)$$
$$= \pi_1(x) + \left[\pi_1(x) \cdot \pi_2(x) \right] + \left[\pi_1(x) \cdot \pi_3(x) \right].$$

To investigate the relationship between predictions of overall reproductive success and independent variables, we examined scatter plots by using Cleveland's robust locally weighted regression algorithm (LOWESS; Cleveland 1979). We also examined, graphically, the results of partial models predicting overall reproductive success with respect to (1) the duration of the guardian period (Age) and (2) the number of other postguardian nests in the colony when adults shifted to postguardian nest attendance (Nests; all other variables held constant at their average values). To predict the nestling age at which the shift to postguardian nest attendance is associated

with the highest overall reproductive success, we set the derivative of the partial model to zero and solved for Age. By altering the seasonal probability of raven presence in the partial model (CORA was held constant at average or at other predicted values), we were able to evaluate how variation in predation pressure influences fitness trade-offs and the behavioral shift to postguardian nest attendance. Unless otherwise indicated, the results are reported as means ± SD.

RESULTS

NEST SUCCESS

The best-performing model used to predict nest success was the global model (Table 4), suggesting that the Great Egret's shift to postguardian nest attendance is a complex behavioral response, based on nestling age (Age), the number of unguarded nests in the colony (Nests), the presence of resident ravens (CORA), and the intraseasonal timing of nest attempts (Egg date). Simpler models of adaptive nest attendance that were worthy of consideration as viable predictors of nest success included the number of other postguardian nests in the colony (per capita risk of nest predation), nestling age, and their interaction (models 3 and 4, Table 4). Therefore, the most likely models of nest success were consistent with both the starvation trade-off and the predation-risk dilution hypotheses.

The odds of nest success were greater if egrets shifted to postguardian nest attendance when there were more unguarded nests in the colony (Nests; Table 5), providing support for the predation-risk dilution hypothesis. Nestling age at the onset of postguardian behavior (Age) had relatively less influence on nest success across all models, and the interaction between the number of unguarded nests in the colony and nestling age had no detectable influence on the odds of nest success (Nests × Age; Table 5). As expected, nest success

TABLE 4. Information criteria for logistic regression models of successful ($n = 936$) vs. unsuccessful (196) Great Egret nests at Bolinas Lagoon, 1984–2008. The number of parameters (K, including the constant, indicator variables for year and covariates in all models for the presence of resident ravens [CORA] and Julian date of the first egg [Egg date]), difference in Akaike's information criterion for small sample size (ΔAIC_c), and Akaike weights (w_i), and Hosmer–Lemeshow goodness-of-fit statistic ($\hat{C}$, df = 8) are provided. Only models with $\Delta AIC_c < 5$ are presented, representing the 0.99 model confidence set ($\sum w_i$). Interactions are indicated by "×."

Model	K	ΔAIC_c[a]	w_i	Hosmer–Lemeshow $\hat{C}$	p
Global	26	0.00	0.78	13.1	0.11
Age, Nests	21	3.67	0.13	5.9	0.66
Age, Nests, Age × Nests	22	4.23	0.09	7.6	0.48

[a] AIC_c of best model = 754.73.

TABLE 5.   Predictor variables in logistic regression models of successful (n = 936) vs. unsuccessful (n = 196) Great Egret nests at Bolinas Lagoon, 1984–2008. Model-averaged odds of predicted nest success, 95% confidence intervals (CI), and the relative importance of each variable ($\sum w_i$ for all models in which each variable occurred) are provided. See Table 2 for definitions of variables.

Variable	Odds	95% CI		$\sum wi$
		Lower	Upper	
Age	1.073	0.99	1.17	1.00
Nests	1.209	1.01	1.45	1.00
CORA × Age	1.009	<1.00	1.02	0.78
CORA × Nest	1.002	0.99	1.02	0.78
Egg × Age	1.000	<1.00	>1.00	0.78
Egg × Nests	1.000	<1.00	>1.00	0.78
Age × Nests	0.999	<1.00	>1.00	0.87
CORA	0.015	<0.01	0.89	1.00
Egg date	0.932	0.91	0.96	1.00

declined with the presence of resident ravens (CORA) and intraseasonal delays in nest initiation (Egg date; Table 5).

PRODUCTIVITY OF SUCCESSFUL NESTS

The best-performing model used to predict the number of young produced in successful nests was model 5, suggesting that egrets were likely to produce more young in successful nests if they shifted to postguardian nest attendance when nestlings were young (Tables 3 and 6). This

TABLE 6.   Information criteria for generalized ordinal logistic regression models of number of young produced in successful Great Egret nests (n = 181, 642, and 112 nests with 1, 2, and 3 young, respectively) at Bolinas Lagoon, 1984–2008. The number of parameters (K, including the constant, indicator variables for year and covariates in all models for the presence of resident ravens [CORA] and Julian date of the first egg [Egg date]), difference in difference in Akaike's information criteria for small sample size (ΔAIC_c), and Akaike weights (w_i), and the multinomial goodness-of-fit statistic ($\hat{C}_g$, df = 16; Fagerland et al. 2008) are provided. Only models with ΔAIC_c < 5 are presented, representing the 0.99 model confidence set ($\sum w_i$). The averaged model, $g(x)$, included predictors for the age of the oldest nestling at the onset of the postguardian period (Age) and the number of other postguardian (unattended) nests in the colony when parental behavior shifts to postguardian nest attendance (Nests). Interactions are indicated by "×."

Model	K	ΔAIC_c[a]	w_i	$\hat{C}_g$	P
				Multinomial goodness of fit	
Age, age × egg date	21	0.00	0.90	8.1	0.94
Global	26	4.73	0.09	8.2	0.94
Age, age × CORA	21	9.61	0.01	7.8	0.95

[a] AIC_c of best model = 1318.66.

TABLE 7.   Predictor variables in logistic regression models predicting the incremental odds of producing additional young in successful Great Egrets nests at Bolinas Lagoon, 1984–2008 (n = 118, 642, and 112 nests with 1, 2, and 3 young, respectively). Model-averaged odds of predicted nest success, confidence intervals (CI), and the relative importance of each variable ($\sum_{wi}$ for models in which the variable occurred) are provided. See Table 2 for definitions of variables.

Variable	Odds	Lower 95% CI	Upper 95% CI	$\sum w_i$
Age	0.926	0.90	0.96	1.00
Nests	0.995	0.95	1.04	0.09
Cora × age	1.005	<1.00	1.01	0.09
Cora × nests	0.996	0.99	>1.00	0.09
Egg date × age	1.000	<1.00	>1.00	0.99
Egg date × nests	1.000	<1.00	>1.00	0.08
Age × nests	1.000	<1.00	>1.00	0.09
CORA	3.741	0.24	59.45	1.00
Egg date	0.939	0.92	0.95	1.00

outcome is consistent with the starvation trade-off hypothesis and fitness benefits of increased foraging time in the postguardian period. This model included an interaction between intraseasonal timing and nestling age, although the interaction was of no detectable importance when averaged across all models (Egg date × Age; Table 7). As in the analysis of nest success, the global model was relatively important in predicting productivity in successful nests (Tables 4 and 6), suggesting that the shift to postguardian nest attendance reflects a complex behavioral response involving elements of both the starvation trade-off and predation-risk dilution hypotheses.

The model-averaged odds of producing additional young in successful nests increased when egrets shifted to postguardian nest attendance earlier in the nesting cycle, relative to the age of developing nestlings (Table 7). As expected, the number of young in successful nests declined with intraseasonal delays in nest initiation (Egg date; Table 7).

OVERALL REPRODUCTIVE SUCCESS

The results for overall reproductive success (number of young fledged per nest attempt) revealed fitness trade-offs in the timing of postguardian nest attendance. Partial models of overall reproductive success predicted the adaptive timing of the shift from guardian to postguardian nest attendance with respect to nestling age (Fig. 1, Table 8). The predicted number of young fledged in any nest attempt increased with the age of nestlings at the time when adults shifted to postguardian nest attendance—up to a threshold, after which productivity declined with further delays in postguardian behavior.

The mean length of guardian nest attendance among the observed nests was 22.0 ± 6.6 days (n = 1132). The combined model of overall reproductive success predicted

TABLE 8.   Model-averaged logit equations used to predict overall reproductive success (number of young produced per nest attempt) of Great Egrets at Bolinas Lagoon, 1984–2008 (see text for structure of the combined model). See Table 2 for definitions of variables.

Successful vs. unsuccessful nests

$g_1(x) = 35.199 - 4.210$ (CORA) $- 0.070$ (Egg date) $+ 0.071$ (Age) $+ 0.190$ (Nests) $+ 0.007$ (Age × CORA) $+ 0.0016$ (Nests × CORA) $+ 0.00005$ (Age × Egg date) $+ 0.0003$ (Nests × Egg date) $- 0.0008$ (Age × Nests)

Successful nests producing two or more young vs. one young

$g_2(x) = 0.921 + 1.319$ (CORA) $- 0.063$ (Egg date) $- 0.077$ (Age) $- 0.0004$ (Nests) $+ 0.0004$ (Age × CORA) $- 0.00034$ (Nests × CORA) $- 0.0001$ (Age × Egg date) $+ 0.000005$ (Nests × Egg date) $- 0.00002$ (Age × Nests)

Successful nests producing three young vs. less than three young

$g_3(x) = -3.876 + 1.319$ (CORA) $- 0.063$ (Egg date) $- 0.077$ (Age) $- 0.0004$ (Nests) $+ 0.0004$ (Age × CORA) $- 0.00034$ (Nests × CORA) $- 0.0001$ (Age × Egg date) $+ 0.000005$ (Nests × Egg date) $- 0.00002$ (Age × Nests)

that egrets would achieve maximum reproductive success if they shifted to postguardian nest attendance when the oldest nestling was 19.9 days old, if (on the basis of average values) they initiated nesting on 18 March, ravens were present on 63% of days during nesting, and there were 10.5 postguardian nests in the colony (Fig. 1). By holding CORA constant at values reflecting 50%, 75%, and 100% raven occurrence, the model predicted that egrets would achieve maximum reproductive success by decreasing or increasing the length of the guardian period to 13.3 days, 24.8 days, and 36.7 days, respectively, in response to differences in the presence of ravens (Fig. 1). This prediction is consistent with the starvation trade-off hypothesis.

The combined model suggested slight benefits in overall reproductive success to breeding pairs that shift to postguardian nest attendance when more nests in the colony are unattended (dilution of per capita risk of nest predation; Fig. 2). In addition, the potential cost of an earlier shift to postguardian behavior, or the potential benefit of a later shift, increased with a greater likelihood that ravens would be present in the colony (Fig. 2), as predicted by the predation-risk dilution hypothesis.
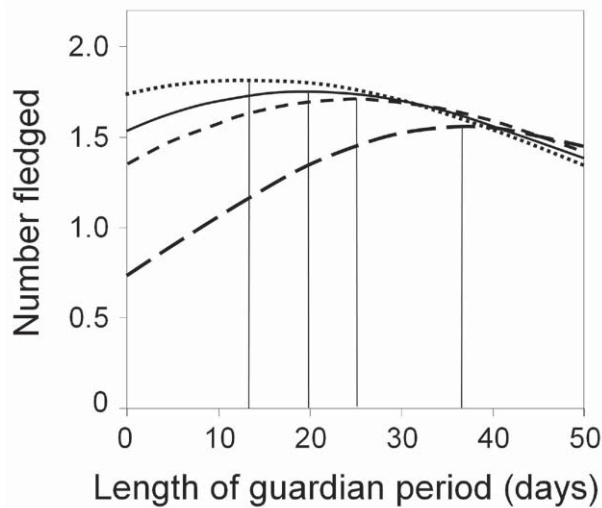

FIGURE 1.   Partial models of overall reproductive success (predicted number of young fledged per nest attempt) with respect to the length of the guardian period of nest attendance (other variables held constant at mean values), based on the predictive equations in Table 8. Lines represent predictions associated with the observed presence of ravens in the colony on 63% of days (solid line), 100% of days (long-dashed line), 75% of days (short-dashed line), and 50% of days (dotted line). Vertical reference lines indicate the predicted length of the guardian period associated with maximum potential reproductive success (100% daily presence of ravens: 36.7 days; 75% presences of ravens: 24.8 days; observed, 63% presence of ravens: 19.9 days; 50% presence of ravens: 13.3 days).
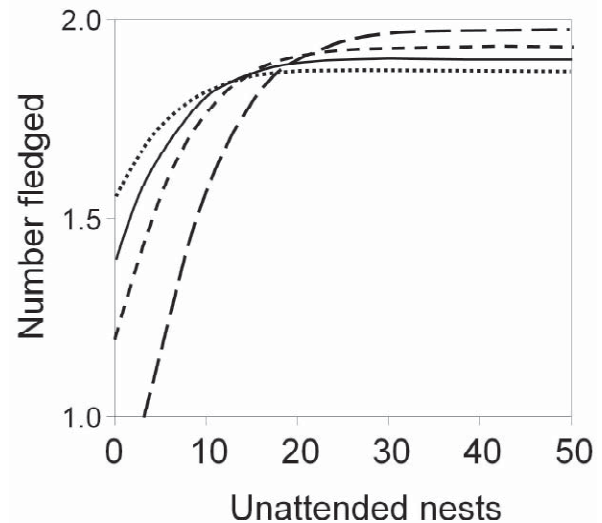

FIGURE 2.   Partial models of overall reproductive success (predicted number of young fledged per nest attempt) with respect to the number of unattended nests in the colony at onset of postguardian nest attendance (other variables held constant at mean values), based on the predictive equations in Table 8. Lines represent predictions associated with the observed occurrence of ravens in the colony on 63% of days (solid line), 100% of days (long-dashed line), 75% of days (short-dashed line), and 50% of days (dotted line).

DISCUSSION

Our results provide support for both the starvation trade-off and predation-risk dilution hypotheses. In addition, parental decisions about the timing of the postguardian period appear to affect nest success and nest fecundity in different ways. For the Great Egret, the risk of nest predation is an important factor in determining the timing of the postguardian period because predation accounts for most nest failure in this system and the attendance of an adult at the nest almost always precludes predation (Martin 1992, Kelly et al. 2005). Strong theoretical support exists for grouping behavior reducing colonially nesting birds' risk of predation (Hamilton 1971, Wittenberger and Hunt 1985). One explanation for this reduced risk is group defense against predators (Picman et al. 1988, 2002), although long-term monitoring at the Martin Griffin Preserve heronry has not revealed mobbing of Common Ravens by Great Egrets, even when the ravens are depredating a nearby nest (Audubon Canyon Ranch, unpublished data).

Another explanation for reduced predation risk in groups is the effect of dilution, or sharing of risk by a greater number of potential prey or nests (Foster and Treherne 1981). In Black-crowned Night-Heron (*Nycticorax nycticorax*) colonies, nests with near neighbors are less likely to be depredated than those that are farther from other nests, and synchronous dummy nests containing eggs are less likely to be depredated than asynchronous nests (Bellinato and Bogliani 1995). Dilution of predation risk has been demonstrated in a colony of the Gray-headed Albatross (*Thalassarche chrysostoma*) where Brown Skuas (*Catharacta lonnbergi*) specialized on predation of the albatrosses' chicks (Catry et al. 2006b). Synchronous timing in the shift to postguardian nest attendance also occurs in Cory's Shearwater (*Calonectris diomedea*), even though dates of laying by close neighbors were no more synchronous than those at nests that were farther apart (Catry et al. 2006a, 2009). The incremental fitness advantages suggested by our results, of reducing per capita predation risk by delaying postguardian nest attendance until more nests are left unattended, would eventually decline to negligible levels or, alternatively, be outweighed by opportunities to reduce nestlings' starvation risk. In addition, egrets might shift to postguardian nest attendance even if the risk of nest predation increases, if reduced starvation risk leads to a net improvement in potential overall fitness.

The risk of predation to unattended Great Egret nests is greatest immediately after the onset of postguardian behavior, when nestlings are relatively small and less likely to successfully deter predators (Kelly et al. 2005). Therefore, the dilution of predation risk is greatest immediately after other unattended nests have reached the postguardian stage. As a result, the potential fitness advantages of delayed nesting to facilitate a delayed shift in postguardian nest attendance, until other unattended nests are available to share the risk of nest predation, is greatest if the behavioral shift occurs soon after other pairs reach the postguardian stage. The time-sensitivity

of such benefits in potential fitness may contribute to the synchronization of not only nest-attendance patterns, but also of nest initiations among colonial nesting birds (Wittenberger and Hunt 1985, Ims 1990, Catry et al. 2009). Successful Great Egret nests that entered the postguardian period when the chicks were younger tended to fledge more young than successful nests guarded until the chicks were older. When both adults leave the nest unattended, they are able to forage for food simultaneously and, therefore, may be able to provide sufficient food to a larger brood. This increased ability to provision nestlings with food may reduce the extent of brood-size reduction and explain why nests entering the postguardian period when nestlings are younger tend to fledge more young. Nestling condition and intraseasonal timing (date), rather than nestling age, are the most important determinants of brood-guarding behavior by the Gray-headed Albatross (Catry et al. 2006b). The length of the nest-guardian period studied by Catry et al. (2006b) seems to be determined primarily by date within the nesting season, but it can be fine-tuned with regard to the nestling's body mass (Catry et al. 2006b), which correlates with age.

In other species, birds nesting early tend to be more successful in fledging young (Smith and Moore 2005, Cooke et al. 1984, Perrins 1970). This pattern has been related to earlier nesting by older, more experienced adults (Nisbet et al. 1984). The intraseasonal timing of nesting by egrets and herons and other bird species has been further associated with the timing of seasonal food supplies needed to support females' formation of eggs (Lack 1954, Perrins 1970, Kushlan 1981, Butler 1993). Therefore, the patterns revealed by our results, suggesting that nests initiated later in the season, on average, exhibit lower nest survivorship and, if successful, fledge fewer young, may depend in part on the age or experience of the adults and/or the intraseasonal timing of available food.

Interestingly, at nests that avoided predation, the model-averaged odds of fledging additional young also *increased*, in relation to the main effect of raven presence (Table 7). One possible explanation for this is that food availability may have been greater in years when ravens were present, reducing the extent of nestling starvation. However, we did not investigate this possibility. Alternatively, the length of the guardianship period may be altered when ravens are present such that some other, unknown, cause of brood reduction is reduced. As above, however, we lack sufficient information to substantiate this or other explanations for this result.

Breeding behavior is mediated by trade-offs in fitness between competing reproductive strategies (Raihani and Ridley 2007). At least two simultaneous mechanisms, influencing components of fitness in different ways, underlie the nest-attendance choices by Great Egrets. As the number of postguardian nests in the colony increases and the per capita risk of nest predation declines, the decision to increase foraging effort by initiating postguardian nest attendance may allow egrets to raise larger broods. As nestlings grow larger, becoming less vulnerable to nest predators and requiring more food to

balance their energy needs, the decision to shift to postguardian nest attendance may allow egrets to optimize trade-offs in potential fitness between guarding the nest against predators and leaving the nest unattended to gather food for nestlings. These mechanisms are consistent with the hypothesis that trade-offs exist between nest success and nest fecundity, illustrated by the combined effects of both models in this study.

Many potentially important influences on nest attendance were not accounted for in this study. These include variation in the age, nesting experience, and foraging skills of adult egrets, variation in clutch size and initial brood size, and variation in the body condition, food demand, and begging intensity of nestlings. Because of the tendency for predators to take prey on the margins of a group, future analyses should account for the spatial position of each nest in the colony (Krause 1994) as a possible influence on patterns of nest attendance. Nests surrounded by immediate neighbors that have reached the postguardian period may be less susceptible to predation, as demonstrated by Schauer and Murphy (1996) for raven predation of Common Murre (*Uria aalge*) eggs. Nest-site characteristics that either facilitate or constrain the predatory movements of ravens or other nest predators, such as foliage cover or the spacing of branches, might account for additional differences in nest attendance. However, Catry et al. (2009) found no measurable effect of nest-site characteristics on nestling guarding by Cory's Shearwaters.

Based on our results, the conservation implications of adaptive nest attendance by Great Egrets include predicted climate-induced changes in the quantity or quality of the surrounding wetlands where the birds feed (Bildstein et al. 1991, Schindler 1997, Day et al. 2008). Climate-induced reductions in the extent of suitable feeding areas may lead not only to the direct effects of reduced food availability on reproductive performance (Kelly et al. 2008), but also to fitness trade-offs that force birds to shorten nest-guardian periods and, consequently, become more vulnerable to nest predators.

The introduction or intensified presence of native or non-native nest predators, such as feral cats, ravens, and raccoons, might force nesting birds to delay postguardian nest attendance, sacrificing postguardian foraging time and their ability to provision nestlings, and reducing the number of young fledged from successful nests. Similarly, herons and egrets often nest near human activity (Kelly et al. 2007). If egrets perceive repeated direct disturbance by humans or the increased presence of construction or other human activities as an increase in predation risk (Frid and Dill 2002), they may increase the length of the nest-guardian period, reducing postguardian foraging time and the number of young fledged from successful nests. The results of our study suggest that environmental influences on nesting behavior might alter mechanisms of reproductive success needed to sustain the growth or resilience of populations, and should be considered carefully by preserve managers.

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