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Brood Provisioning and Nest Survival of *Ardea herodias* (Great Blue Heron) in Maine

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Abstract - From 1983–2009, the number of coastal breeding pairs of *Ardea herodias* (Great Blue Heron [GBHE]) in Maine declined by 64%, and the number of occupied islands on which these birds bred declined by 40%. The Maine Department of Inland Fisheries and Wildlife listed the GBHE as a species of special concern in 2007, and expanded its annual monitoring to include inland colonies in 2009. To assess regional demographic differences, we compared the relationship between brood provisioning and nest survival of GBHEs in 1 coastal and 1 inland colony. In terms of brood-provisioning within the 2 colonies, the inland colony had significantly greater rates for the first 2 weeks post-hatch, but the coastal colony had greater rates in subsequent weeks. These differences did not affect either nest fate (≥1 chick fledged) or daily nest survival at the inland or coastal colony. In both colonies, the maximum number of nestlings observed at a nest was positively correlated with the number that subsequently fledged. Daily nest survival was positively associated with an increasing number of nestlings, earlier hatch dates, and increased brood-provisioning rates for 1–2-week-old chicks. Our results suggest that the number of nestlings per nest can be used as a proxy for nest survival in GBHE colonies in the northeastern part of their range. Furthermore, because nest survival was influenced by brood-provisioning rates during the first 1–2 weeks post-hatch, our results suggest that the most sensitive time for disturbance of GBHEs in the northeastern part of their range may be earlier in the nesting stage than previously thought.

Introduction

Between 1960 and 2008, the human population inhabiting the coast of Maine increased by 62.2%, and housing units in coastal counties increased 106.4% (US Census Bureau 2008). From 1983–2009, the number of coastal breeding pairs of *Ardea herodias* L. (Great Blue Heron [GBHE]) in Maine declined by 64% (2.46% annually), and the number of occupied islands on which these birds breed declined by 40% (1.54% annually) (D'Auria 2009). Likewise, between 1983 and 2009, the Breeding Bird Survey (BBS) indicated a 66.3% decline of GBHEs in Maine (2.55% annually; Sauer et al. 2012). In 2007, the Maine Department of Inland Fisheries and Wildlife (MDIFW) listed the GBHE as a species of special concern. Starting in 2009, MDIFW began monitoring wading birds, including GBHE, by conducting both aerial and ground surveys of locations determined by the historical distribution of GBHE colonies as well as information from citizen scientists and state biologists.

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Available evidence suggests that GBHEs select a specific colony location based on proximity to a productive food source (Gibbs 1991, Gibbs et al. 1987, Kirsch et al. 2008) and distance from potential human and predator disturbances (Carlson and McLean 1996, Norman et al. 1989, Parnell et al. 1988, Todd et al. 1982, Vos et al. 1985). Islands in Maine with or without a GBHE colony tend to be in similar proximity to profitable foraging areas; however, occupied islands were farther from human populations (Gibbs 1991, Gibbs et al. 1987). With increasing human development in coastal areas, potential colony locations that are both free of disturbance and close to productive food sources are becoming rare. Although data have been presented about coastal breeding sites, little is known about factors affecting the population dynamics of inland colonies in Maine, primarily due to logistical challenges the state had in monitoring these inland colonies.

In 2012, we initiated a preliminary study to understand demographic differences between a coastal and an inland GBHE colony in Maine. We assumed that coastal birds were moving to increase provisioning rates of chicks and predicted that feeding rates of chicks would be higher at inland colonies than coastal colonies. Furthermore, we predicted that higher brood-provisioning rates would result in higher nest-survival rates at the inland colonies.

Methods

Study area

During the 2012 breeding season, there were 87 active GBHE colonies in Maine, with 940 breeding pairs (D'Auria, MDIFW, Bangor, ME, pers. comm.). In 2012, the MDIFW reported 13 coastal colonies with an average of 27.6 nests per colony (± 32.2 SD) and 74 inland colonies with an average of 8.7 nests per colony (± 10 SD). We focused on 1 inland colony (IN) in southern Maine between Long and Highland Lakes in Bridgton, ME (44°4'44.56"N, 70°42'25.55"W) and 1 near-shore coastal-island colony (CO) in Brunswick, ME (43°51'45.29N, 69°54'21.17"W); both colonies were on private property (Fig. 1). We selected these 2 sites due to the large number of breeding pairs (inland: 56, coastal: 40), comparable acreages (IN: 2.4 ha; CO: 1.35 ha), and accessibility.

Field methods

We placed 5 Trekker® T-200 ground blinds (173 cm L x 173 cm W x 165 cm H), 3 at CO and 2 at IN, to conduct focal behavioral observations. To limit disturbance, we set up the blinds in March before birds arrived at the sites. We assigned each nest a unique number and conducted nest observations using a Nikon® ProStaff fieldscope (82-mm body, 20–60x zoom eyepiece) and, depending on the distance of the nest from the blind, 10 x 42 or 8 x 40 Nikon Monarch® binoculars.

Brood-provisioning observations

Four observers (M.M. Meserve and 3 volunteer field technicians) monitored all active nests in both the IN and CO colonies; 2 observers were in a blind during all observation periods. Observation periods lasted for 6 h every 3 days from 14 April

to 25 May, 9 h every 4 days from 26 May to 5 June, and 6 h every 3 days from 6 June to 24 July (Table 1). A comprehensive review of human-disturbance effects on nesting colonial waterbirds suggested limiting our surveys of GBHE colonies to no more than once every 3 d (Carney and Sydeman 1999); due to our small sample size (2 colonies) and the observed sensitivity during the 26 May–5 June time period,
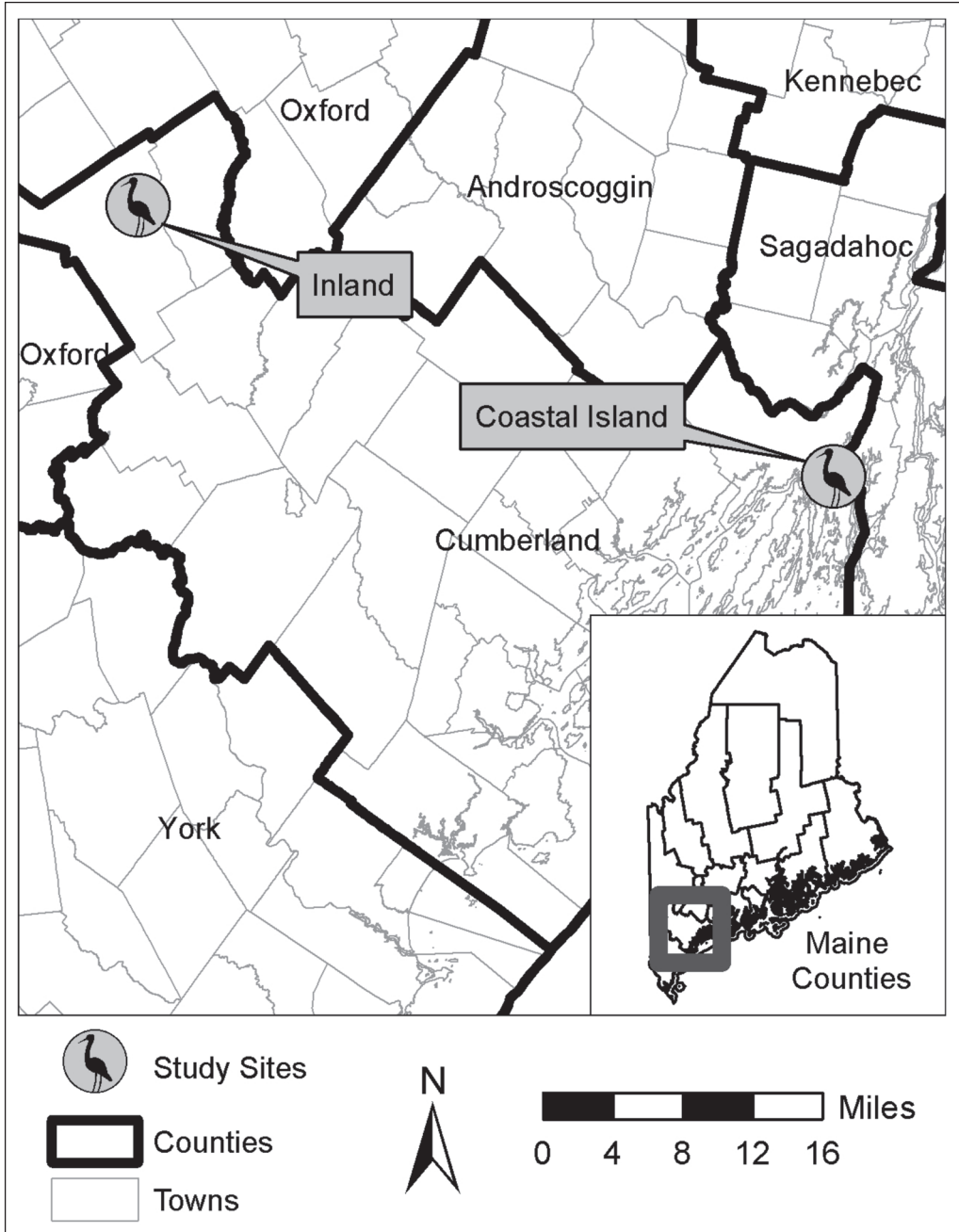

Figure 1. Location of 2 Great Blue Heron colonies monitored in southern Maine in 2012.

we utilized a 4-d rotation to minimize our disturbance at the colonies (Carney and Sydeman 1999, Vennesland and Butler 2004), while still allowing for adequate data collection. We continued observations until the last fledgling left each colony: 13 July for CO, and 24 July for IN.

We habituated the birds to our presence by slowly approaching the area of the observation blind and stopping if a bird flushed or began to "chortle" or "cluck" (Vennesland and Norman 2006). Once the birds settled, observers continued to the blind. During each focal observation, we recorded the nest number, status (active or inactive), and stage (incubating, nestlings, fledglings), as well as the number and stage of nestlings (1–2, 2–4, 4–6, or 6–8 weeks old). Each observer conducted 3-h focal-observation periods for each nest in succession. Observers rotated through nests numerically and only skipped a nest if it was inactive (no longer contained any nestlings); we classified a nest as inactive when there was no evidence of adults, nestlings, or fledglings for an entire observation day.

Daily nest survival

We used the Program MARK nest-survival module (Rotella et al. 2004, White and Burnham 1999) to evaluate daily nest survival (DNS), determine if daily nest survival differed between the IN and CO colonies, and identify what ecological and behavioral factors best explained variation in DNS. We considered a nest to be successful if it fledged ≥1 young. We tested the effect of 7 covariates on DNS: hatch date; average number of feeding trips per hour across the entire nestling stage (average brood-provisioning rate [AvgBP]); average brood-provisioning rate within the first 2 weeks (AvgBPa), 2–4 weeks (AvgBPb), 4–6 weeks (AvgBPc), and 6–8 weeks (AvgBPd) post-hatch; and total number of hatchlings (defined as the maximum number of nestlings seen in a nest at any stage). Age was determined using the nestling illustrations from Vennesland and Norman (2006). We ran all possible one-way, interactive, and additive models, and ranked competing models by their corrected (for small sample size) AIC_c values. AIC_c is a second-order correction for AIC that is computed as,

$$AIC_c = -2(\text{log-likelihood}) + 2k + (2k[k + 1]) / (n - k - 1),$$

where n = number of observations and k = number of parameters (Burnham and Anderson 2004). We then calculated ∆AIC for each model, which measured the difference in AIC_c between model i and the best-fitting model. We also calculated the

Table 1. Nest-observation rotation schedule used to monitor an inland (IN) and coastal (CO) Great Blue Heron colony in Maine. am = morning, pm = afternoon.

| | | | | | Day number | | | | | | |
Schedule	1	2	3	4	5	6	7	8	9	10	11
6-hour	IN	CO	-	IN	CO	-	IN	CO	-	IN	CO
Time of day	am	am	-	pm	pm	-	am	am	-	pm	pm
9-hour	IN	CO	-	-	IN	CO	-	-	IN	CO	-
Time of day	am	am	-	-	pm	pm	-	-	am	am	-

AIC$_c$ weight (w_i), interpreted as the probability of any model being the best model in the model set. We considered models with $\Delta AIC_1 < 2$ to have substantial support in explaining variation in the data (Burnham and Anderson 2004).

Statistical analysis: Brood-provisioning rates and effects of number of nestlings present

We conducted separate one-way analysis of variance (ANOVA) tests to assess any differences between the CO and IN colonies in: nestling age (using the age of the oldest chick), age-specific brood-provisioning rates, and the number of nestlings per nest. To test differences between AvgBPa, AvgBPb, AvgBPc, and AvgBPd, we used Kruskal-Wallis tests because these data did not fit the assumptions of normality and equal variance needed for an ANOVA. We conducted an ANOVA with pairwise comparisons for both IN and CO colonies to determine the relationship between brood-provisioning rates by nestling age class. We used Pearson product-moment correlations to look for relationships between number of nestlings within a nest, brood-provisioning rates, and number of chicks fledged within a nest.

Results

Daily nest survival

Nest survival for the IN colony was 68% (95% CI = 50–81%) and 49% (43–55%) for the CO colony. Daily nest survival was 0.996% (95% CI = 0.998–0.993%) and 0.993% (0.994–0.991%) for the IN and CO colonies, respectively. Two competing models best explained variation in daily nest survival (Table 2). The interaction between the number of nestlings and hatch date best explained variation in DNS, and had 1.7 times more support than the second-ranked model (Table 2). The additive model including the number of nestlings and AvgBPa was the second-ranked model (Table 2). The number of nestlings in a nest was an additive or interactive factor in the highest-ranked models, accounting for $w_i = 0.610$. Post-hatching daily nest survival increased as both the number of nestlings increased and hatch date decreased (Fig. 2A, B). Post-hatching daily nest survival also increased with the combination of a higher AvgBPa and an increased number of nestlings (Fig. 2C, D).

Table 2. Our 5 highest-ranked program MARK nest-survival models for Great Blue Herons breeding in Maine, 2012, listed in order of their Akaike weights (w_i).

Model	Deviance	ΔAICc	K	w_i	Evidence ratio
Number of nestlings*Hatch date	158.46	0.000	4	0.286	3.497
Average brood-provisioning rate for 1–2-week-old chicks + Number of nestlings	161.53	1.076	3	0.167	5.988
Average brood-provisioning rate for 1–2-week-old chicks* Number of nestlings	160.92	2.473	4	0.083	12.048
Average brood-provisioning rate for 1–2-week-old chicks* Hatch date	161.16	2.703	4	0.074	13.514
Average brood-provisioning rate for 1–2-week-old chicks+ Site	163.52	3.058	3	0.062	16.129

Brood-provisioning rates

We observed 21 nests at the CO colony between 14 April and 13 July, and 29 nests at the IN colony between 17 April and 24 July. We conducted a total of 411 observation hours (IN = 216 h, CO =195), and observed 64 brood-provisioning events at the IN colony and 59 at the CO colony. Both IN and CO colonies had similar hatch dates, numbers of chicks per nest, and showed the highest feeding rates in the youngest age class, and these rates consistently decreased with increasing nestling age (Fig. 3). AvgBPa in the IN colony was significantly greater than AvgBPb (t_{27} = -4.767, $P < 0.001$); AvgBPc (t_{20} = -4.672, $P = 0.0001$), and AvgBPd (t_{32} = -5.057, $P < 0.001$). There was no significant difference in the brood-provisioning rates as the season progressed for the CO colony ($F_{1,3}$ = 0.806, $P = 0.496$). We found no correlation between the brood-provisioning rate for a nest and the number of nestlings within that nest (IN: R^2_{22} = 0.067, $P = 0.76$; CO: R^2_{13} = 0.461, $P = 0.08$; combined: R^2_{37} = 0.305, $P = 0.06$). There was no correlation between colony and brood-provisioning rate (R^2_{44} = 0.269, $P = 0.07$) or between brood-provisioning rate and nest fate (R^2_{44} = -0.196, $P = 0.19$).

Both the IN and CO colonies fledged 1.1 young per nest (IN = 1.11, CO = 1.09). The average number of nestlings per nest did not differ between colonies—IN: mean = 2.6, SD = 1.1, CO: mean = 3.1, SD = 1.0 ($F_{1,33}$ = 1.379, $P = 0.249$; Fig. 4). The number of nestlings within a nest was positively associated with the number that fledged for both colonies (IN: R^2_{27} = 0.173, $P = 0.025$; CO: R^2_{19} = 0.438, $P = 0.001$; combined: R^2_{48} = 0.545, $P < 0.001$; Fig. 5).
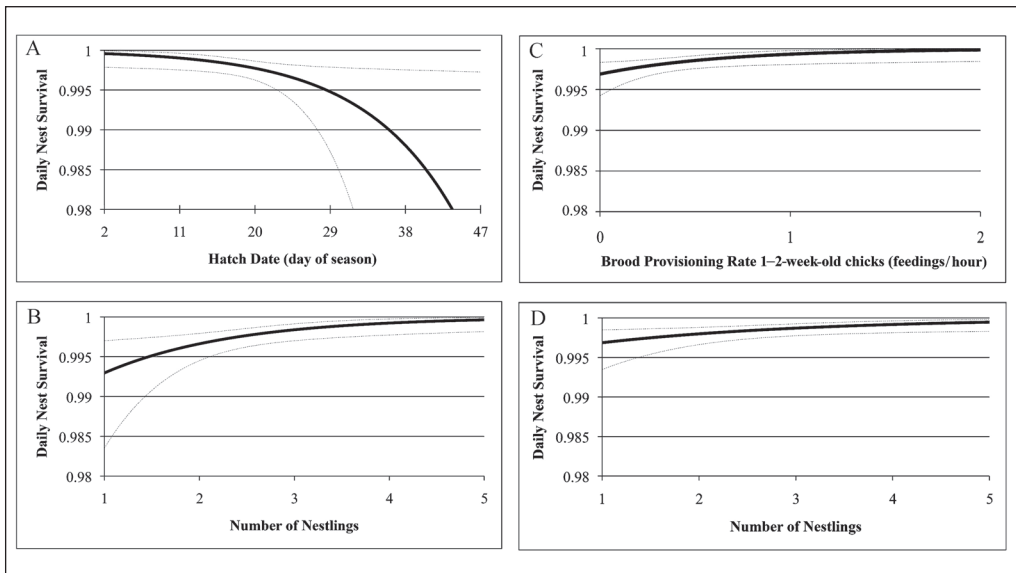

Figure 2. Daily nest-survival rates (DSR) of Great Blue Heron nests in southern Maine based on the interactive models of hatch date (day of season) (A) and number of nestlings (B), and the additive models of brood provisioning rate of 1–2-week-old chicks (C) and number of nestlings (D). The dotted lines indicate the 95% confidence intervals.

Discussion

We predicted lower daily nest survival at coastal colonies compared to inland colonies to explain the decline of GBHE nesting in coastal Maine, potentially as a consequence of lower brood-provisioning rates at coastal sites. However, we did
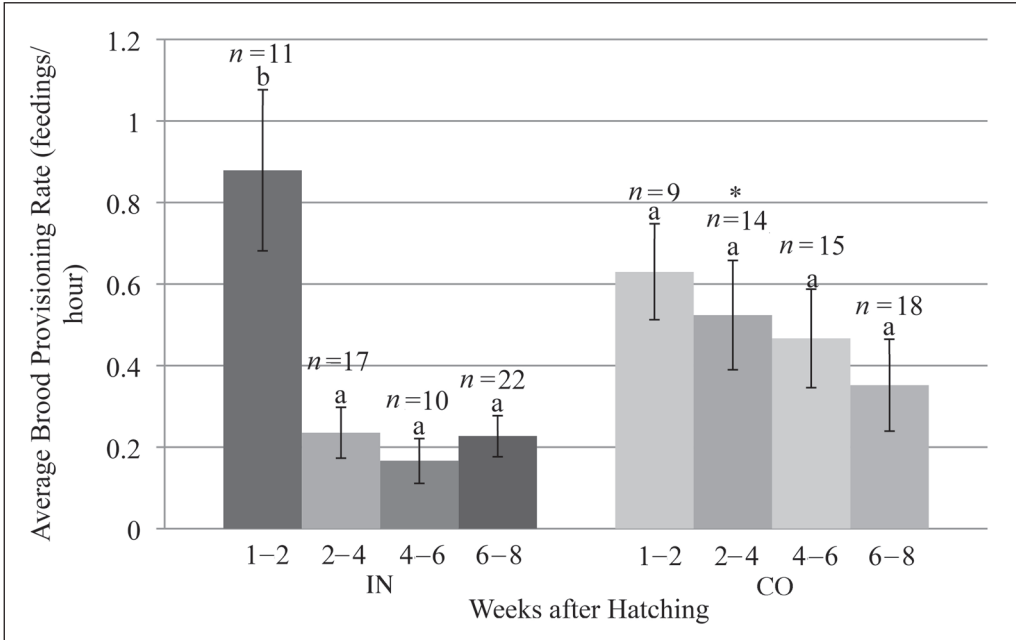

Figure 3. Average brood-provisioning rates during 4 time intervals at 2 Great Blue Heron colonies (IN = inland, CO = coastal) in southern Maine in 2012. Error bars indicate standard error, letters denote statistical differences within sites based on an ANOVA with pairwise comparisons, and * indicates a significantly greater provisioning rate between sites.
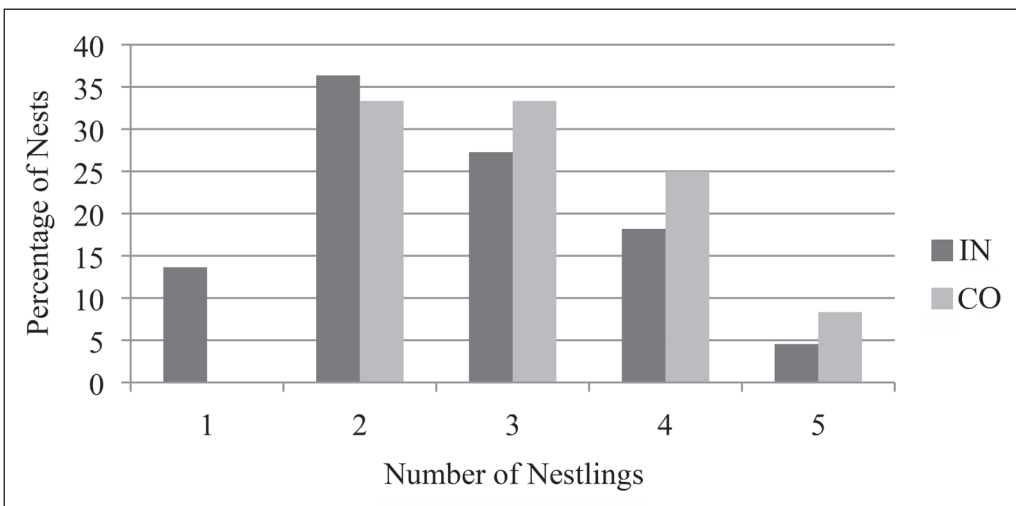

Figure 4. Percent of Great Blue Heron nests with 1–5 nestlings at an inland (IN: $n = 29$) and coastal (CO: $n = 21$) colony in Maine in 2012.

not detect any variation in daily nest survival between the 1 coastal and 1 inland colony we studied. Instead, variation in daily nest survival across all nests was best explained by the interaction between the number of nestlings and hatch date. We also found that higher brood-provisioning rates within the first weeks post-hatch were positively associated with daily nest-survival rates. Our results are contrary to past studies that documented differences in wading-bird reproductive success and breeding phenology between 2 different habitat types. For example, *Ardea cinera* L. (Grey Heron) in northern Poland nest in both inland and coastal colonies, and Jakubas (2011) found that coastal Grey Herons began nesting and hatching earlier than their inland counterparts. Frederick et al. (1992) found that fledging success of *Egretta thula* Molina (Snowy Egret) and *Egretta tricolor* Muller (Tricolored Heron) in southern Florida was higher in freshwater rather than saline habitats. Although we found no variation in nest survival between colonies, we acknowledge that we monitored only 2 colonies. Therefore, we suggest future studies investigate more colonies to assess whether other factors (i.e., colony size, landscape characteristics) may affect nest survival at coastal versus inland colonies.

We observed 64 brood-provisioning events at the inland site ($n = 29$ nests) and 59 at the coastal site ($n = 21$ nests). The highest brood-provisioning rates occurred in the first 1–2 weeks post-hatch at both the inland and coastal colonies; feeding rates thereafter declined as the season progressed, a pattern reported in past research (Brandman 1976, Collazo 1981, Pratt 1970). The average brood-provisioning rates for 2–8-week-old chicks at the inland colony appeared lower than those at the coastal colony (Fig. 3); however, feeding rates during these periods did not explain variation in daily nest survival at either colony. Our results might indicate that there was a difference in the quality and/or quantity of food delivered between the colonies, which is a topic for further study.
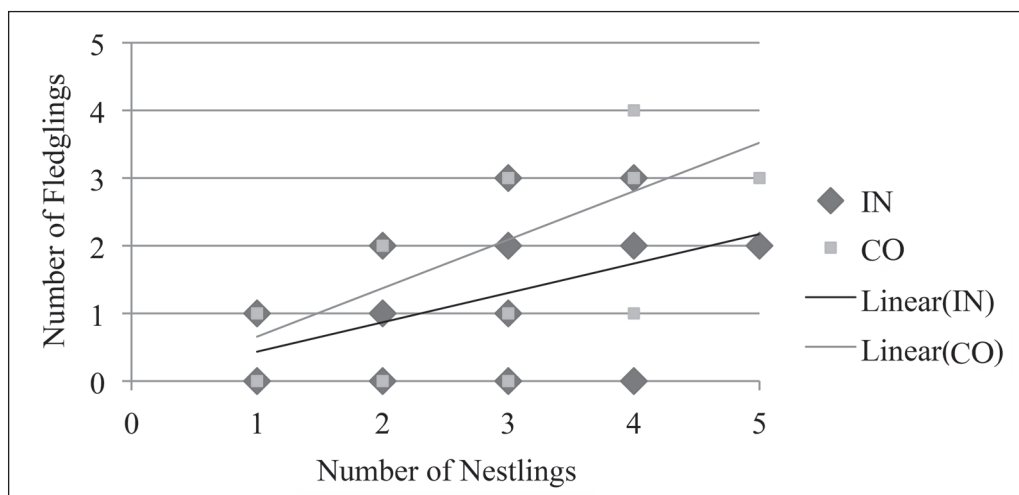

Figure 5. Relationship between the number of Great Blue Heron nestlings and fledglings at an inland (IN) and coastal (CO) colony in southern Maine in 2012 (IN: $R^2 = 0.173$, df = 27, $P = 0.025$, $n = 29$; CI: $R^2 = 0.438$, df = 19, $P = 0.001$, $n = 21$). The lines on the graph represent the linear regression of the data (IN: $y = 0.4342x$; CO: $y = 0.7039x - 0.0183$).

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Our top-ranked model to assess daily nest-survival rates indicated that GBHE daily nest-survival rates would increase if they hatched their young earlier in the season and had more nestlings in the nest. In this study, we were unable to assess clutch size due to nest heights. However, if the number of nestlings in a nest was an accurate reflection of clutch size, our results agree with others who found that pairs that produce more eggs have more fledglings (GBHE: Pratt and Winkler 1985, Grey Heron: Millstein et al. 1970, *Ardea purpurea* L. [Purple Heron]: Tomlinson 1975, and Great Egret: Morrison and Shanley 1978). Furthermore, Butler (1993) found that food availability determined when a female GBHE laid her eggs (Butler 1993, Perrins 1970). Future studies should explore the relationship between clutch size, food availability, and colony location.

The second-ranked model showed that daily nest survival increased when adults fed their young more frequently in the first 2 weeks post-hatch, and when eggs began hatching earlier in the season. Jakubas (2005) found that the number of feeding visits to colonies of Grey Herons was the most important factor affecting breeding success. In California, Pratt (1970) also saw an increase in brood-provisioning frequency during the first 1–2 weeks of life in GBHEs. A study of the energy requirements in hand-reared GBHE nestlings found the greatest energy requirements for growth were between 10 and 29 d post-hatch (Bennett et al. 1995). The discrepancy in the period of time of greatest provisioning demand between Bennett et al. (1995) and Pratt (1970) may be due to the fact that Bennett et al. (1995) studied hand-reared chicks. Our results indicate the most important time period for higher brood-provisioning rates as the first 1–2 weeks post-hatch.

To fully understand the regional population dynamics of Great Blue Herons, monitoring efforts should focus on key times within the breeding season when accurate nestling numbers and ages can be gathered; specifically after the first 1–2 weeks post hatch. Ideally, monitoring efforts should encompass both coastal and inland habitats in order to better understand variation in regional population dynamics, and particular attention should be paid to the hatching times in these colonies. The decline of GBHEs along the coast of Maine could be an indicator of a greater disruption in Maine's coastal ecosystem. With a total of 411 hours of colony monitoring and 123 observed brood-provisioning events, this study is the most thorough examination of parental care and nestling behavior of GBHEs in the northeastern part of its range. Our work provides a more accurate and current estimate of the most sensitive times during the GBHE breeding season in the northeastern part of their range, as well as a way to accurately and non-invasively assess nest survival. These data can serve as a model for monitoring regional waterbird populations including those in Maine.

Acknowledgments

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