Articles

Journal of Avian Biology 47: 399–408, 2016
doi: 10.1111/jav.00900
Published 2015. This article is a U.S. government work and is in the public domain in the USA.
Journal of Avian Biology © 2015 Nordic Society Oikos
Subject Editor: Ronald Ydenberg. Editor-in-Chief: Jan-Åke Nilsson. Accepted 28 October 2015

The effects of heterospecifics and climatic conditions on incubation behavior within a mixed-species colony

Peter S. Coates, Brianne E. Brussee, Roger L. Hothem, Kristy H. Howe, Michael L. Casazza and John M. Eadie

P. S. Coates (pcoates@usgs.gov), B. E. Brussee, R. L. Hothem, K. H. Howe and M. L. Casazza, U.S. Geological Survey, Western Ecological Research Center, Dixon, CA, USA. – J. M. Eadie and BEB, Dept of Wildlife, Fish, and Conservation Biology, Univ. of California, Davis, CA, USA.

Parental incubation behavior largely influences nest survival, a critical demographic process in avian population dynamics, and behaviors vary across species with different life history breeding strategies. Although research has identified nest survival advantages of mixing colonies, behavioral mechanisms that might explain these effects is largely lacking. We examined parental incubation behavior using video-monitoring techniques on Alcatraz Island, California, of black-crowned night-heron *Nycticorax nycticorax* (hereinafter, night-heron) in a mixed-species colony with California gulls *Larus californicus* and western gulls *L. occidentalis*. We first quantified general nesting behaviors (i.e. incubation constancy, and nest attendance), and a suite of specific nesting behaviors (i.e. inactivity, vigilance, preening, and nest maintenance) with respect to six different daily time periods. We employed linear mixed effects models to investigate environmental and temporal factors as sources of variation in incubation constancy and nest attendance using 211 nest days across three nesting seasons (2010–2012). We found incubation constancy (percent of time on the eggs) and nest attendance (percent of time at the nest) were lower for nests that were located < 3 m from one or more gull nest, which indirectly supports the predator protection hypothesis, whereby heterospecifics provide protection allowing more time for foraging and other self-maintenance activities. To our knowledge, this is the first empirical evidence of the influence of one nesting species on the incubation behavior of another. We also identified distinct differences between incubation constancy and nest attentiveness, indicating that these biparental incubating species do not share similar energetic constraints as those that are observed for uniparental species. Additionally, we found that variation in incubation behavior was a function of temperature and precipitation, where the strength of these effects was dependent on the time of day. Overall, these findings strengthen our understanding of incubation behavior and nest ecology of a colonial-nesting species.

Nesting is considered a critical life phase that regulates population dynamics among avian species (Martin 1993), and the success of nesting is largely dependent on parental incubation behavior (Deeming 2002). Environmental conditions that influence incubation behavior have been studied in many species of birds, both solitary (Coates and Delehanty 2008) and colonial breeders (Drent 1970), and effects that have been identified are fundamentally different between life history breeding strategies. Additionally, incubation by uniparental species requires energetic trade-offs as parents must budget time for behaviors associated with self-maintenance versus those of parental care (Conway and Martin 2000a), while biparental species likely have fewer energetic constraints (Bulla et al. 2015). Regardless of breeding strategy, birds can adjust nesting behaviors to account for environmental conditions and reduce the probability of nest predation while simultaneously maintaining optimal conditions for incubation (Ghalambor and Martin 2000, Fontaine and Martin 2006).

In the case of colonial species, social factors likely have substantial effects on parental incubation behavioral patterns. Such factors include the parent's relative position within the colony, density of nests, or distance to the nearest neighbor. For example, colonial nesting could offer protective benefits from conspecifics (Götmark and Andersson 1984) for species with defensive behavior (e.g. predator mobbing), while more docile colonial species may only benefit through dilution of predation risk (Wittenberger and Hunt 1985). Within mixed-species colonies, fundamental differences in life history traits between species likely influence the incubation behavior and nest survival of one or both species. Multiple studies have now demonstrated nest survival advantages of mixed-species colony nesting for more docile species (Veen 1977, Burger 1984, Bogliani et al. 1999). For example, species that exhibit little to no predator-mobbing behavior, such as herons (Forbes 1989), may nest in close proximity to more aggressive species to gain a protective advantage (Quinn and Ueta 2008). Burger (1984) explored a mechanism through which protective species dynamics function, wherein silvery *Podiceps occipitalis* and white-tufted grebe *Rollandia rolland* nesting in brown-hooded

gull *Chroicocephalus maculipennis* colonies benefited from early warning alarm calls of gulls and were able to better conceal nests from predators before fleeing the colony. Furthermore, sandwich terns *Thalasseus sandvicensis*, which primarily sit tight on eggs in the presence of a predator, benefit from anti-predator behavior of common terns *Sterna hirundo* and black-headed gulls *Chroicocephalus ridibundus* to avian predators, namely mobbing and chasing predators from the colony. Although black-headed gulls are a potential egg predator of tern nests, this paradoxical dynamic increases nest success for those terns nesting closer to gulls (Veen 1977). In mixed-species colonies, behavioral decisions of docile species are likely influenced by the balancing of costs versus benefits of nesting close to aggressive species.

We conducted a multi-year study (2010–2012) to investigate ecological factors that affect incubation behavior of nesting black-crowned night-herons *Nycticorax nycticorax* (hereinafter night-herons) on Alcatraz Island, California. This colonial nesting species was chosen for this study because of three major advantages: 1) the nesting ecology of the colony is well-understood (Hothem and Hatch 2004, Hothem et al. 2013) on this island, as well as knowledge of the egg predators, namely common ravens *Corvus corax* (Hothem et al. 2013), 2) night-herons are a docile species and usually nest in close proximity to western gulls *L. occidentalis* and California gulls *L. californicus*, of which both gull species are relatively aggressive; and 3) the island offered accessibility to nesting colonies of night-herons and gulls to evaluate mixed-species interactions using advanced video-monitoring techniques.

The principle objective of this study was to explain variation in incubation behavior of night-herons by investigating effects of heterospecifics, climatic conditions, within-season temporal effects, and other ecological factors. Our study consisted of multiple a priori hypotheses. First, we hypothesized that incubation behavior was influenced by proximity to heterospecifics. Specifically, night-herons in close proximity to gull nests would exhibit riskier parental behaviors (e.g. reduced nest attendance) than those not located within the mixed-species colony. Furthermore, we predicted that the influence of this proximity to heterospecifics effect would be greater than effects of density of night-heron nests within the colony, given that herons are a docile species that do not exhibit predator-mobbing behaviors (van Vessem and Draulans 1986), and known security advantages associated with mixed-species colonies (Veen 1977). Second, we hypothesized that this species would exhibit little evidence of energetic constraints during incubation based on their biparental incubation life history strategy (Bulla et al. 2015) and, thus, climatic conditions (e.g. increased precipitation) would not influence incubation behavior. Third, we hypothesized a lack of evidence for seasonal temporal effects in incubation behaviors because nesting by night-herons on Alcatraz Island is not synchronous but instead initiated over an entire season (Hothem and Hatch 2004). We also quantified specific daily nesting behaviors of night-herons and hypothesized that these birds exhibit predictable diel patterns in incubation behaviors, with less risky incubation behaviors (e.g. action that could alert a visually-cued predator such as ravens) occurring during daylight periods when predation pressure was greatest.

Methods

Study area

Alcatraz Island (37.8°N, 122.4°W) is a 9.1 ha island located in the San Francisco Bay, approximately 1.6 km north of San Francisco, California, and has been managed by the National Park Service since 1973. The island provides important breeding habitat for many avian species within the San Francisco Bay area (Howell and Pollak 1991, Kelly et al. 1993, Saenz et al. 2006). Night-herons were first documented on the island in 1975 (Bradley 2005) and other species that occupy the island include common ravens *Corvus corax*, western gulls, and California gulls. Historic buildings, roads, remnants of demolished buildings, as well as vegetation such as century plant *Agave americana*, mirror plant *Coprosma repens*, rose *Rosa* spp., fuchsia *Fushia* spp., English ivy *Hedera helix*, ice plant *Carpobrotus* spp., eucalyptus *Eucalyptus* spp., and cypress *Cupressus macrocarpa* characterize the island. Breeding season temperatures average from 4–16°C in the beginning of March to 12–20°C in July. The majority of annual precipitation occurs from January to March, ranging from approximately 9 cm in early breeding season (i.e. March) to <0.5 cm later in the breeding season (i.e. June and July).

Field methods

We conducted intensive island-wide searches on a weekly basis from mid-April through late July of 2010−2012, during which we sought to locate night-heron nests in the early stages of incubation (i.e. <7 d elapsed from first egg laid). At each nest, we recorded coordinates using a handheld Global Positioning System (UTM, North American Datum 1983), as well as the dominant nesting substrate (Table 1), which consisted of the six categories: blackberry *Rubus* spp., fuchsia, English ivy, karo *Pittosporum crassifolium*, century plant, and rubble piles of demolished buildings (i.e. scrap metal, wood, reinforcing rods, and other debris).

We installed video systems on a random sample of night-heron nests stratified by dominant vegetation types. We monitored nests continuously (24-h d^{-1}) using micro-cameras consisting of seven infrared (950 nm wavelength) light-emitting diodes (30×110 mm with a 3.6-mm lens; EZ Spy Cam, Los Angeles, CA) and Digital Video Recorders (DVRs). Cameras were concealed using camouflage duct tape and vegetation, and were installed on sturdy vegetation or on a camouflaged iron stake 0.5–1.0 m from the selected nest. We used 100 m coaxial cables to connect cameras to 4-channel H.264 DVRs (AV Tech, Hong Kong, China). Each DVR system was camouflaged. Nests with cameras were monitored weekly to confirm nest fates.

During the weeks of 7 June and 14 June in 2011, and 7 May in 2012, we recorded precise locations of every California and western gull nest on the island on high-resolution paper topographic maps to investigate the effects of mixed colony nesting on night-heron incubation behavior. Gull nesting data were not collected in 2010 because of timing constraints.

Table 1. Explanatory variables used to develop incubation behavior models for black-crowned night-herons nesting on Alcatraz Island, 2010–2012.

Group description	Model	Description
Year	YR	Year
Light period	LP	Light period
Temporal	INIT	Ordinal date of nest initiation (elapse from 1 January)
	AGE	Day of incubation (for 25-d incubation time)
	ORD	Ordinal date (elapse from 1 January)
	ORDSEAS	Number of days since first nest initiation of season
Weather	TMIN	Minimum temperature (°C) experienced over video-day
	TMAX	Maximum temperature (°C) experienced over video-day
	PRCP	Presence or absence of precipitation over video-day
Nest characteristics	HAB	Substrate
	NESTS	Density of nests m^{-2} in nesting areas
	VICIN[a]	Presence/absence of a gull nest ≤ 3 m of night-heron nest
	GULL10[a]	Count of gull nests ≤ 10 m buffer

[a]Gull metrics were only measured in 2011 and 2012.

Quantifying night heron incubation time budgets

We reviewed video data and quantified specific night-heron incubation behaviors across a random selection of dates, ensuring at least one calendar date of quantified behavioral data for each monitored nest (1–10 calendar days per nest). We excluded days within 24 h of nest failure or hatch, as well as dates when we visited the island for monitoring. We chose a random sample of video recordings per nest to measure behavior because random sampling strategies provide reliable estimates of incubation behaviors (Davis and Holmes 2012). Specifically, we randomly assigned two 10-min time intervals per hour to examine diel patterns for each behavior to assure uniform sampling throughout each day.

Within the 10-min intervals, we measured the percent of time (seconds) the bird was engaged in two general behaviors: incubation constancy and nest attendance. Incubation constancy was defined as the act of sitting on the eggs with physical contact between the parent and eggs, and nest attendance included time spent at the nest site without contact with eggs. We considered a nest attended if the heron was within the field of view of our camera, generally a meter surrounding the nest. We explored both incubation constancy and attendance because each behavior may represent distinct processes (Coates and Delehanty 2008). For example, if incubation constancy and attendance are aligned, as is likely the case for uniparental species, that would signify that time spent not incubating must be spent foraging to maintain energy reserves for incubation (Tulp and Schekkerman 2006). Conversely, if there is a decoupling of incubation constancy and attendance, wherein birds are on their nest but not engaging in egg maintenance, then we can assume minimal energetic constraints on the parent bird. Therefore, factors influencing incubation constancy identify those conditions during which a night-heron can be present on the nest without incubating, while those factors that influence attendance identify conditions when night-herons are more likely to be off the nest (e.g. low predation pressure).

We also recorded a second tier of more specific behaviors consisting of vigilance (defined as scanning the surrounding environment), preening, nest maintenance, and inactivity. These additional behaviors provide information about how night-herons utilize time spent on their nests, when more active behaviors (preening or nest maintenance) could be considered risky (more likely to signal a visually-cued predator). Birds that spend more time inactive would be considered less risky in terms of predation (Martin et al. 2000). Although a parent can engage in only one specific behavior at a time, a parent can simultaneously engage in general behaviors and a specific behavior. For example, a parent can be incubating eggs while vigilant on the nest.

Because daily temporal rhythms often play an important role in regulating behaviors in birds, we assigned each 10-min interval to one of six daily light periods based on sunrise and sunset data (National Oceanic and Atmospheric Administration). To generate the six periods, we first calculated the amount (min) of daylight as the difference in time from sunrise to sunset and divided this number by three to create three equal daylight periods (early light [EL], mid-light [ML], and late light [LL]). Similarly, we calculated the amount of nighttime to create three equal night periods (early dark [ED], mid-dark [MD], and late dark [LD]). Thus, sunrise marked the change from LD to EL, while sunset marked the change from LL to ED. This accounted for varying length of daylight as the nesting season progressed. The average times that correspond to the onset of EL, ML, LL, ED, MD, and LD were 06:00, 10:45, 15:30, 20:15, 23:30, and 02:45, respectively. For those 10-min intervals that overlapped two light periods, the interval was divided at the cut-time between the two intervals. Data for each behavior variable were averaged across all 10-min intervals per light period per day. Statistical analyses were conducted on the nest-day-light periods scale.

Statistical analyses

We modeled the two general incubation behaviors (incubation constancy and nest attendance) as response variables. We developed generalized linear mixed effects models (Zuur et al. 2009) to evaluate fixed effects (e.g. environmental and temporal factors) while fitting a random effect (i.e. individual bird) to account for correlation in repeated measurements and unbalanced sampling across birds (Gillies et al. 2006).

Each response variable was modeled separately with multiple covariates described in Table 1. Categorical predictors in the model included light period, nest substrate, and year. Temporal effects consisted of covariates for ordinal date of nest initiation (days elapsed since 1 January), age of nest (day of incubation for a 25-d period), ordinal date (days elapsed since 1 January), and date of behavioral data since first initiation of season (days elapsed since first initiation of season). Data on temperature and precipitation were obtained from a weather station located in nearby San Francisco, CA (37.7°N, 122.4°W; U.S. National Climate Data Center, Asheville, North Carolina). We included average daily precipitation (mm), minimum and maximum daily temperature (°C) as weather covariates.

In a Geographic Information System (GIS), we imported nest locations to calculate average night-heron nest densities within the corresponding nesting area boundary. We also digitized locations of all gull nests into a GIS to measure the presence of gull nests directly related to each night-heron nest by counting gull nests contained within a 10-m buffer scale centered on each night-heron nest. Additionally, we developed a categorical variable describing presence or absence of a gull nest within a 3-m buffer area centered on each night-heron nest (Table 1). Spatial analyses were conducted using Geospatial Modeling Environment (Beyer 2012) and Spatial Analyst tools in ArcGIS 10.1 (ESRI).

Our statistical analysis procedure was based on techniques described by Coates and Delehanty (2010). For each response variable, we carried out a two-step analysis. The first step compared models that consisted only of variables measured during all three years of the study (2010–2012; hereafter, referred to as 'full dataset'). We examined single-variable models, as well as additive effects (two-variable combinations) where no correlations were identified. We generated a correlation matrix between all covariates and excluded those that co-varied ($r \geq |0.65|$) to reduce the effects of multicollinearity (Dormann et al. 2013). We included interactions between light period and weather covariates to better understand how conditions throughout the day influence incubation behaviors. To compare support among models (n = 68), we calculated Akaike information criterion (AIC) adjusted for finite sample size (c), differences in AIC_c values (Δ; Anderson 2008), and Akaike weights (w_i) to evaluate models (Anderson 2008). We also calculated a linear mixed effects model conditional R^2 ($R^2_{LMM[c]}$) that describes the proportion of variance explained by both fixed and random effects, and marginal R^2 ($R^2_{LMM[m]}$) that describes the proportion of variance explained only by the fixed effects (Nakagawa and Schielzeth 2013). This first step allowed us to rank models by their support from the data for incubation behaviors using data collected during all three years of the study. Covariates that garnered support from this step were carried forward to a second modeling step by meeting two criteria: 1) the covariate was included in the best model from the model set (e.g. lowest AIC_c), and 2) the model that included the covariate was 2 ΔAIC_c less than the null (intercept-only model).

During step two, we restricted the dataset (hereafter, referred to as 'restricted dataset') to form models (incubation constancy, n = 14; attendance, n = 10) using covariates carried forward from step one and the additional covariates associated with nesting gulls from data collected during 2011 and 2012. Similar to the approach used with the full dataset, we examined single-variable models as well as additive effects (two variables) where no correlations were identified, and included interactions between light period and the weather covariates. Again, we limited our combinations to two covariates to reduce the total number of models in our final data set. This second step allowed us to examine whether the variables describing nesting gulls provided greater explanation of incubation behaviors than those variables measured across the three year study period. All analyses were conducted using program R ('lme4' package, Bates and Maechler 2010). Conditional and marginal R^2 for linear mixed effects models (Nakagawa and Schielzeth 2013) were calculated using the MuMIn package (Barton 2014).

Data available from the ScienceBase Repository: <http://dx.doi.org/10.5066/F7TT4P1K> (Coates et al. 2015).

Results

Daily time budget

We quantified incubation behavior using 211 video-monitored nest days across 81 nests (17 in 2010, 30 in 2011, and 34 in 2012). The average incubation constancy for night-herons across a 24-h period was 94.0% (CI: 92.5–95.5%, Fig. 1A). However, night-herons demonstrated considerable differences in incubation constancy across light periods, with the lowest incubation constancy occurring during the mid-light period (90.6%; CI: 89.2–92.1%) and the highest during the late light period (96.4%; CI: 95.6–97.2%, Fig. 1A). Nest attendance patterns were different from that of incubation (Fig. 1B). Nest attendance averaged 98.3% (CI: 97.1–99.4%) across the 24-h period, but had substantially less variation than incubation constancy across light periods. During the first two light periods, incubation constancy was relatively low even though birds were still attending their nests (Fig. 1A and B).

Night-herons exhibited clear diel patterns in specific behaviors. We found that birds were inactive 82.3% (CI: 81.2–83.6%) of early light period hours, and 93.2% (CI: 92.0–94.4%) of the early dark period (Fig. 2A). Vigilance was, on average, highest during the early light periods (5.2%; CI: 4.4–5.9%) and mid-light periods (5.0%; CI: 4.2–5.7%; Fig. 2B). Similarly, preening was most often exhibited during the mid-light period (2.8%; CI: 2.4–3.1%; Fig. 2C) and nest maintenance was, on average, highest during the early light period (5.7%; CI: 5.1–6.2%; Fig. 2D). Night-herons exhibited low levels of vigilance, preening, and nest maintenance during the nighttime hours (Fig. 2B, 2C, and 2D).

Full dataset

The full dataset included data for 211 video-monitored nest days across 81 nests (17 in 2010, 30 in 2011, and 34 in 2012).The most parsimonious model of the 68 models evaluated for incubation constancy consisted of light period interacting with maximum daily temperature and precipitation ($w_{LP \times TMAX + LP \times PRCP} = 0.98$; Table 2). This model predicted: 1) decreased incubation constancy with increas-

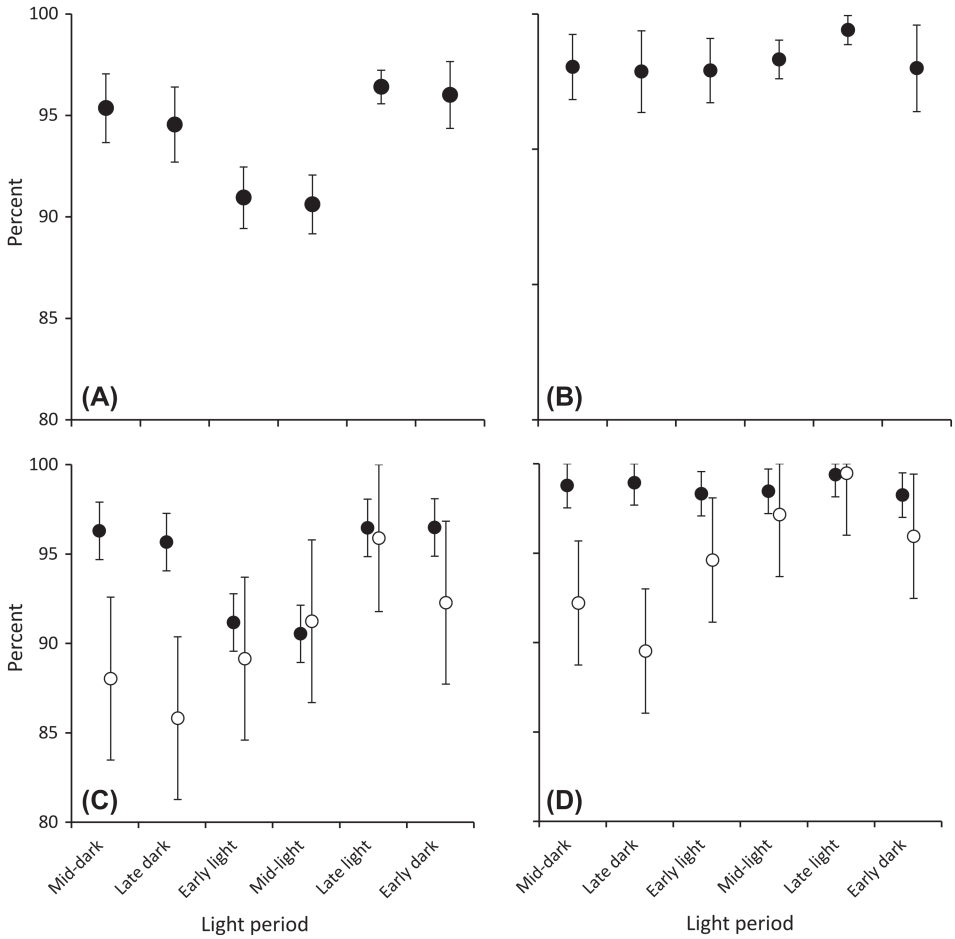

Figure 1. For each light period, average percent (A) incubation constancy and (B) nest attendance and model predicted percent (C) incubation constancy and (D) attendance by precipitation presence (open circle) and absence (closed circle) of black-crowned night-herons nesting on Alcatraz Island 2010–2012. Vertical bars are confidence intervals.

ing maximum temperature during the early and mid-light periods, with little effect during late light, early dark, mid-dark, and late dark periods (Fig. 3); and 2) decreased incubation constancy during mid-dark and late dark periods on days with precipitation, with no effect during the other light periods (Fig. 1C). The light period covariate was found in all of the top models explaining incubation constancy. The only temporal covariate within the top models for incubation constancy was the age covariate appearing in an additive model with light period. This model predicted an 18.0% (CI: 0.0–34.5%) increase in incubation constancy for every one day increase in nest age. Overall, based on the $R^2_{\mathrm{LMM[c]}}$ value the full model (fixed and random effects) explained nearly 50% of the variation in incubation constancy, and much of the explained variance was attributed to differences among individuals (Table 2; Nakagawa and Schielzeth 2013).

The most parsimonious model of the 68 models evaluated for nest attendance was an interaction between light period and precipitation ($w_{LP\times PRCP}=0.95$; Table 3). This model predicted lower nest attendance during the mid-dark and late dark light periods on days with precipitation, and no effect of precipitation on nest attendance during the other four light periods (Fig. 1D). The precipitation covariate occurred in all of the top five models explaining nest attendance. Nest attendance was lower overall on days with precipitation (94.8%; CI: 93.3–96.3%) than on days with no precipitation (98.7; CI: 98.5–98.9%). Light period only occurred in the top models as an interaction with weather covariates. In fact, the single-variable model including light period performed worse than the null model in the model set for nest attendance. Nest density occurred in one of the top models as an additive model with precipitation; however, this model did not outperform the single variable model with precipitation. This indicates that nest density did not explain any additional variation in nest attendance. No temporal covariates or nest site characteristics were found to be influential for nest attendance in the full dataset.

Restricted dataset

The restricted dataset included data from 126 nest-days across 64 nests (30 in 2011, and 34 in 2012). Of the 24 models analyzed using the restricted dataset, the most parsimonious model for explaining incubation constancy included those interactions found to be important from the full dataset (Table 2; LP × TMAX + LP × PRCP), as well

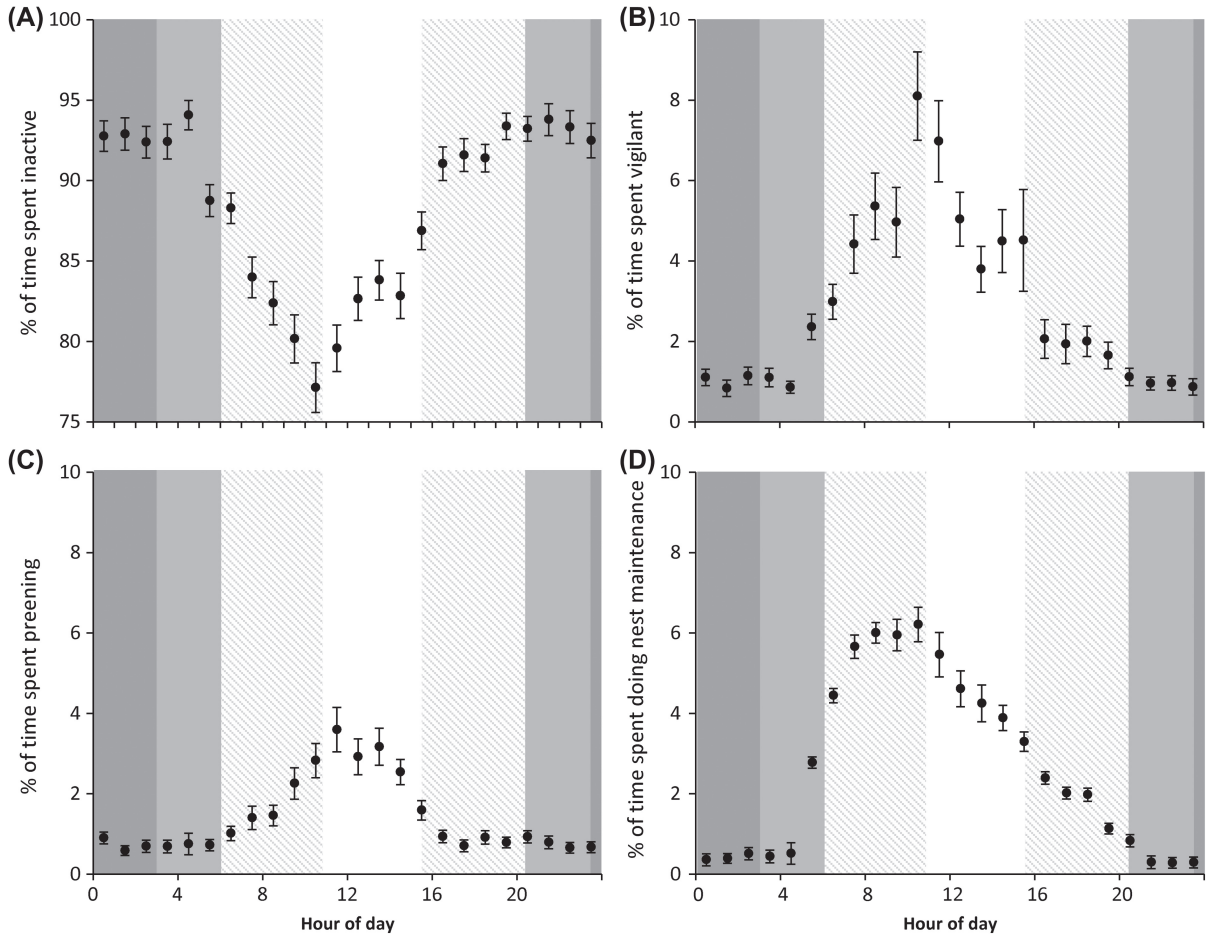

Figure 2. Average percentage of time spent (A) inactive, (B) vigilant, (C) preening, and (D) and doing nest maintenance by black-crowned night-herons (nests = 81) on Alcatraz Island 2010–2012. Vertical bars are standard errors. Shading represents light periods (EL and LL, shaded diagonal lines; ML, white; ED and LD, light grey; MD, dark grey).

Table 2. Model selection for incubation constancy of black-crowned night-herons nesting on Alcatraz Island 2010–2012. logLik = Log(*Likelihood*); K = number of estimated parameters; ΔAIC_c = difference (Δ) in Akaike's information criterion (AIC_c) between best approximating model and model of interest with second order bias correction; w = model probability. $R^2_{LMM[m]}$ (marginal) describes proportion of variance explained by the fixed effects, whereas $R^2_{LMM[c]}$ (conditional) describes the proportion explained by both fixed and random effects (Nakagawa and Schielzeth 2013).

Model[a]	Explanatory variables[b]	K	logLik	ΔAIC_c	w	$R^2_{LMM[m]}$	$R^2_{LMM[c]}$
Step 1							
1	LP × TMAX + LP × PRCP	21	–4660.9	0.00	0.98	0.08	0.48
2	LP × PRCP	15	–4671.1	8.14	0.02	0.06	0.47
3	LP × TMAX	15	–4676.7	19.26	0.00	0.06	0.47
4	LP + AGE	10	–4686.8	29.31	0.00	0.05	0.46
5	LP + PRCP	10	–4687.0	29.72	0.00	0.05	0.46
Null		4	–4734.5	112.61	0.00	NA	NA
Step 2							
6	LP × TMAX + LP × PRCP + VICIN	22	–2735.0	0.00	0.51	0.11	0.54
7	LP × TMAX + VICIN	16	–2742.3	1.95	0.19	0.10	0.53
8	LP × PRCP + VICIN	16	–2742.7	2.85	0.12	0.09	0.53
9	LP × VICIN	15	–2743.9	3.20	0.10	0.09	0.53
10	LP × TMAX + LP × PRCP	21	–2738.6	5.03	0.04	0.08	0.54
Null		4	–2790.5	74.63	0.00	NA	NA

[a]Step 1 compared models (n = 68) within the full dataset (nests, n = 81), which included variables measured from 2010–2012. Step 2 compared models (n = 24) using a restricted dataset (nests, n = 64), which consisted of the covariates from the best model from the full dataset with additional variables from measurements taken from 2011–2012. The five most parsimonious models were listed in table, as well as a null model (consisted of random effects only) for comparative purposes.
[b]All models consisted of a random effect for individual birds.

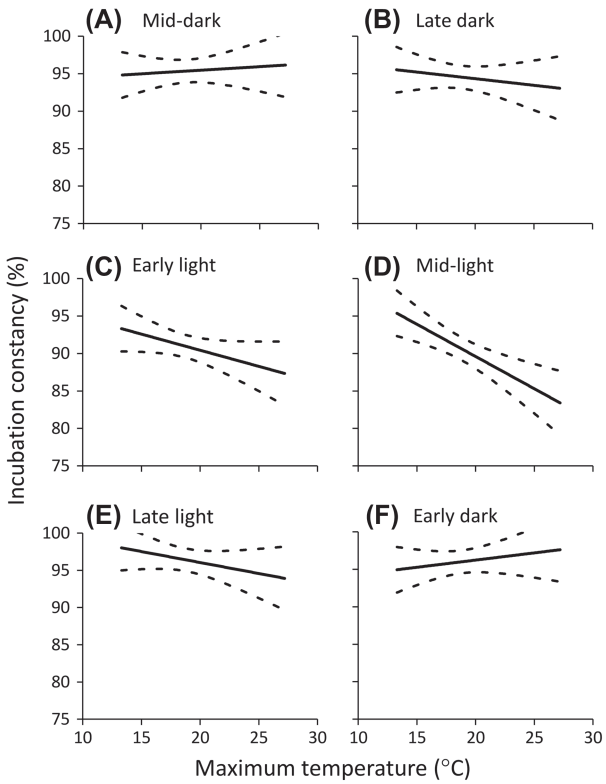

Figure 3. The estimated effect of maximum temperature (°C) and light period on incubation constancy (percent) of black-crowned night-herons nesting on Alcatraz 2010–2012 based on model results from the full dataset. Dotted lines are confidence intervals.

as the covariate that represented the presence of a nesting gull within 3 m of a night-heron nest (VICIN, $w_{LP \times TMAX + LP \times PRCP + VICIN} = 0.50$). Based on the calculated $R^2_{LMM[m]}$ the addition of the VICIN covariate explained variation in the data that was not represented by the light period and climate interactions alone (Table 2), and the full model represented >50% of variation in incubation constancy ($R^2_{LMM[c]}$). Specifically, this model predicted that incubation constancy was 4.1% (CI: 1.7–6.5%) lower in nests within 3 m of a gull than those further away (Fig. 4A).

Restricting the nest attendance dataset to allow investigation of gulls, we found the VICIN covariate was also important for explaining variation in nest attendance (Table 3). Of the 16 models analyzed using the restricted dataset, the best model for describing nest attendance included an interaction with light period and precipitation with the additive gull effect ($w_{LP \times PRCP + VICIN} = 0.72$; Table 3). This model was more explanatory than the next best model that included only the interaction of light period and precipitation, and predicted a 1.7% (CI: 0.4–2.9%) decrease in attendance in nests within 3 m of a gull nest (Fig. 4B).

Discussion

This study identified clear and predictable diel patterns of incubation behavior in a colonial nesting species. It also demonstrated how behavior relates to nest age, multiple environmental factors, as well as proximity to nesting heterospecifics. Increased incubation constancy increases the probability of successful nesting in night-heron populations, therefore knowledge of factors that explain variation in incubation behaviors contribute to understanding the relative fitness of night-heron (Brussee 2013).

Most importantly, to our knowledge, we identified the first empirical evidence of the influence of one nesting species on the incubation behavior of another in a mixed-species colony. Night-herons nesting in close association with a gull nest (within 3 m) nearly doubled the time spent not incubating (from 5 to 9%), and quadrupled the time that nests were left unattended (from 0.5 to 2%). We expected this influence on incubation constancy given evidence in the

Table 3. Model selection for attendance of black-crowned night-herons nesting on Alcatraz Island 2010–2012. logLik = Log(*Likelihood*); K = number of estimated parameters; ΔAIC_c = difference (Δ) in Akaike's information criterion (AIC_c) between best approximating model and model of interest with second order bias correction; w = model probability. $R^2_{LMM[m]}$ (marginal) describes proportion of variance explained by the fixed effects, whereas $R^2_{LMM[c]}$ (conditional) describes the proportion explained by both fixed and random effects (Nakagawa and Schielzeth 2013).

Model[a]	Explanatory variables[b]	K	LL	ΔAIC_c	w	$R^2_{LMM[m]}$	$R^2_{LMM[c]}$
Step 1							
1	LP × PRCP	15	−4406.5	0.00	0.95	0.04	0.37
2	LP × TMAX + LP × PRCP	21	−4403.5	6.40	0.04	0.04	0.37
3	PRCP	5	−4423.5	13.78	0.00	0.02	0.35
4	PRCP + NESTS	6	−4422.9	14.51	0.00	0.02	0.35
5	AGE + PRCP	6	−4422.9	14.52	0.00	0.02	0.35
Null		4	−4427.9	20.52	0.00	NA	NA
Step 2							
6	LP × PRCP + VICIN	16	−2370.4	0.00	0.72	0.06	0.26
7	LP × PRCP	15	−2373.1	3.13	0.15	0.05	0.26
8	LP × PRCP + GULL10	16	−2372.9	4.99	0.06	0.05	0.26
9	VICIN	5	−2389.0	14.36	0.00	0.02	0.26
Null		4	−2391.4	17.30	0.00	NA	NA

[a]Step 1 compared models (n = 68) within the full dataset (nests, n = 81), which included variables measured from 2010–2012. Step 2 compared models (n = 16) using a restricted dataset (nests, n = 64), which consisted of the covariates from the best model from the full dataset with additional variables from measurements taken from 2011–2012. The five most parsimonious models were listed in table, as well as a null model (consisted of random effects only) for comparative purposes.
[b]All models consisted of a random effect for individual birds.

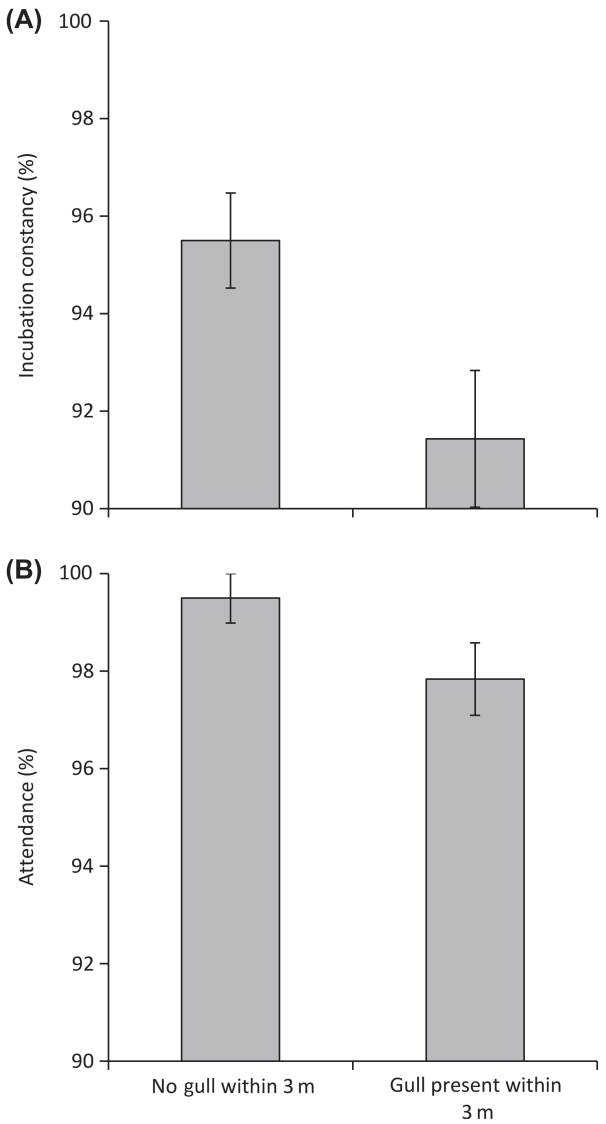

Figure 4. The estimated effect of nesting in close proximity to gull nest on (A), average incubation constancy (percent) and (B), attendance (percent) of black-crowned night-herons nesting on Alcatraz Island 2011–2012 based on model results from the restricted dataset. All other variables were set to their mean. Vertical bars are confidence intervals.

literature that gulls provide protection against nest predation for other species, including savannah sparrows *Passerculus sandwichensis* (Wheelright et al. 1997), and several duck species (Dwernychuk and Boag 1972, Burger 1984, Young and Titman 1986, Väänänen 2000). Veen (1977) found that black-headed gulls and common terns indirectly protected sandwich tern nests that were within 4 m of their own nest, which is consistent with 3 m spatial scale in our analysis. If gulls offer protection of night-heron nests in a similar manner, then additional security may allow night-herons to budget more time on self-maintenance behaviors away from nests rather than those that require vigilance at nest sites. However, this paradoxical source of protection might result in predation of eggs or nestlings by gulls, or kleptoparasitism (Hatch 1970). In other words, the presence of gulls may lead to perceived security and, thus, influence incubation behavior but might not ultimately influence predation rates. Nevertheless, this phenomenon appears to offer advantages for night-herons, as we found no effect of night-heron nest density on incubation behavior suggesting that night-herons gain more protection in mixed-species colonies, than in single-species colonies.

On occasion, we observed night-herons depredate eggs from nests, but this primarily occurred after nest abandonment. Nest abandonment in long-lived species can be an evolved strategy to conserve resources for future reproductive efforts when conditions are suitable (Williams 1966). Given the lack of effect of nest density on incubation behavior we do not expect that the potential for predation by night-herons is of major importance to overall nest success or to nesting behavior.

We expected night-herons to exhibit less risky incubation patterns during daylight periods when predation pressure was greatest. Our hypothesis was based on two sources of information. First, the existing knowledge of the predator community on Alcatraz Island, where the primary predators of night-heron eggs are ravens (Hothem et al. 2013); no mammalian have been observed predating night-herons on the island. Ravens use visual cues while hunting only during daylight hours and depredate most nests during early morning hours (Coates and Delehanty 2008). Secondly, past research has indicated that birds often adjust behaviors based on perceived predation risk (Ghalambor and Martin 2000, Eggers et al. 2008, Lima 2009, Zanette et al. 2011). For example, Siberian jays *Perisoreus infaustus* and two species of nuthatch *Sitta* spp. were found to make fewer trips to provision their offspring when exposed to models of predators (Ghalambor and Martin 2000, Eggers et al. 2006). Indeed, we found that vigilance was highest during the early- and mid-light periods, suggesting that night-herons are more alert to the presence of predators, especially during times when ravens are likely most active in the environment (Luginbuhl et al. 2001). However, contrary to our prediction, other behaviors that might alert ravens, such as nest maintenance and preening were also high during the early- and mid-light periods (Fig. 2). Perhaps the benefits of increasing vigilance during these hours of the day offset more risky behaviors that involve movements at the nest site.

We found incubation constancy decreased with increased temperature. However, this relationship was dependent on the time of day (i.e. interaction). These results are similar to those found for several species of passerines (Whitehouse and Armstrong 1953, Conway and Martin 2000b), wood ducks (Breckenridge 1956), and for arctic shorebirds (Tulp and Schekkerman 2006, Smith et al. 2012), where incubation recesses were longer during the warmest parts of the day. This likely indicates adults capitalizing on warmer temperatures during the early and mid-day, thereby expending less energy on incubation and egg rewarming, and alternatively engaging in self-maintenance activities (Ardia et al. 2009). However, for night-herons and other biparental species this relationship is likely not a result of tradeoffs against parental energy budgets, but might reflect changes in the perception of the needs of the eggs by the parents. For example, temperature was less influential for night-heron nest attendance, indicating that temperature does not affect parental off-bouts for foraging, but rather influences a parent birds' decision of

whether to incubate while present on the nest site. Because parent birds do not maintain constant incubation while on the nest, this suggests that energy constraints to adult night-herons during incubation are nearly irrelevant. Additionally, these findings support those of Bulla et al. (2015), wherein heating of eggs in arctic nests did not result in longer incubation bouts.

Conversely, we found both incubation constancy and attendance were lowest during the nighttime hours (mid-dark) on days with precipitation. Increased temperature and precipitation may provide fundamentally different resources for incubation. For example, given that night-herons are nocturnal foragers (Watmough 1978), they might be taking advantage of optimal foraging in overcast conditions during and after rain events (Bovino and Burtt 1979) and when ravens are less likely to be active (Luginbuhl et al. 2001). Thus, increased temperature appears to benefit eggs, whereas precipitation events are advantageous for parents.

This study was not without constraints. First, we were unable to account for intrinsic factors affecting incubation behavior such as body condition or age of bird. Younger uniparental birds are known to have lower incubation constancy rates than older birds, largely because of fewer endogenous reserves (Aldrich and Raveling 1983, Yerkes 1998). If this is the case for biparental birds, then younger, less-experienced night-herons may be forced to nest closer to areas of increased gull activity, and poorer body condition requires them to forage more often, thereby reducing nest attendance and incubation constancy. However, with the recent evidence of little to no energetic constraints associated with biparental incubation described here and elsewhere (Bulla et al. 2015), we suspect differences in incubation constancy as a function of energy demands among age classes to not be the case for night-herons. Furthermore, in 1996–1997, night-heron nests on Alcatraz numbered around 240 (Hothem and Hatch 2004), whereas in 2010–2012, the average number of night-heron nests on Alcatraz was 141 nests. Therefore, nest site availability likely does not affect night-heron nest placement in relation to gulls.

An additional factor that could regulate the amount of time an adult designates for incubation is food availability, wherein greater food availability allows for more time spent on the nest and less time foraging (Rastogi et al. 2006, Londoño et al. 2008, Ardia et al. 2009). Resources likely vary annually or throughout the incubation period and we found no annual or seasonal effects on incubation behaviors, indicating that night-herons do not necessarily time their nesting around peak forage availability, and thus food availability likely plays a minor role in regulating nesting behaviors for this generalist species. The only temporal factor that was influential to night-heron incubation patterns was nest age. As nest age increased, the probability of making it to hatch also increased, making the nest attempt more valuable to the parent bird, thus parental attentiveness increased (Smith and Wilson 2010).

In this study, we found clear and novel evidence that nesting in proximity to more aggressive colonial-nesting species influences night-herons to exhibit more risky behaviors including decreased incubation constancy. Additionally, incubation behaviors varied according to climatic conditions, and these relationships were dependent on the time of day. Overall, these key ecological relationships contribute to the current understanding of avian nesting ecology within mixed-species colonies.

Acknowledgements – This research was conducted with support from the Golden Gate National Parks Conservancy and the U.S. Geological Survey Western Ecological Research Center. We would particularly like to thank Bill Merkle and Victoria Seher at the National Park Service for their continued support of this research. We would also like to thank Michelle Fearon and Daniel Smith for assistance with fieldwork and video analysis. The use of trade, product, or firm names in this publication does not imply endorsement by the U.S. Government.

References

Aldrich, T. W. and Raveling, D. G. 1983. Effects of experience and body weight on incubation behavior of Canada geese. – Auk 100: 670–679.

Anderson, D. R. 2008. Model based inferences in the life sciences. – Springer.

Ardia, D. R., Pérez, J. H., Chad, E. K., Voss, M. A. and Clotfelter, E. D. 2009. Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behavior. – J. Anim. Ecol. 78: 4–13.

Barton, K. 2014. Package "MuMIn: mulit-model inference". Version 1.14.0. – <http://cran.r-project.org/web/packages/MuMIn/index.html> accessed 1 June 2015.

Bates, D. and Maechler, M. 2010. Package 'lme4'. Version 0.999375-35.532. – <http://lme4.r-forge.r-project.org/> accessed 30 August 2010.

Beyer, H. L. 2012. Geospatial modelling environment. Version 0.6.0.0. – <www.spatialecology.com/gme>.

Bogliani, G., Sergio, F. and Tavecchia, G. 1999. Woodpigeons nesting in association with hobby falcons: advantages and choice rules. – Anim. Behav. 57: 125–131.

Bovino, R. R. and Burtt, E. H. 1979. Weather-dependent foraging of great blue herons (*Ardea herodias*). – Auk 96: 628–630.

Bradley, D. 2005. Cultural landscapes inventory: Alcatraz Island. – National Park Service.

Breckenridge, W. J. 1956. Nesting study of wood ducks. – J. Wildl. Manage. 20: 16–21.

Brussee, B. E. 2013. Nest survival and incubation behaviors of black-crowned night-herons on Alcatraz Island. – MS thesis, Univ. of California, Davis.

Bulla, M., Cresswell, W., Rutten, A. L., Valcu, M. and Kampenaers, B. 2015. Biparental incubation-scheduling: no experimental evidence for major energetic constraints. – Behav. Ecol. 26: 30–37.

Burger, J. 1984. Grebes nesting in gull colonies: protective associations and early warning. – Am. Nat. 123: 327–337.

Coates, P. S. and Delehanty, D. J. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. – Condor 110: 627–638.

Coates, P. S. and Delehanty, D. J. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. – J. Wildl. Manage. 74: 240–248.

Coates, P. S., Brussee, B. E., Hothem, R. L., Howe, K. H., Casazza, M. L. and Eadie, J. M. 2015. Data from: The effects of heterospecifics and climatic conditions on incubation behavior within a mixed-species colony. – Dryad Digital Repository, <http://dx.doi.org/10.5066/F7TT4P1K>.

Conway, C. J. and Martin, T. E. 2000a. Evolution of passerine incubation behavior: influence of food, temperature and nest predation. – Evolution 54: 670–685.

Conway, C. J. and Martin, T. E. 2000b. Effects of ambient temperature on avian incubation behavior. – Behav. Ecol. 11: 178–188.
Davis, S. K. and Holmes, T. G. 2012. Sprague's pipit incubation behavior. – In: Ribic, C. A., Thompson III, F. R. and Pietz, P. J. (eds), Video surveillance of nesting birds. Stud. Avian Biol. Ser. 43. Univ. of California Press, pp. 67–76.
Deeming, D. C. 2002. Behavior patterns during incubation. – In: Deeming, D. C. (ed.), Avian incubation: behavior, environment, and evolution. Oxford Univ. Press, pp. 63–87.
Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Shröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.
Drent, R. H. 1970. Functional aspects of incubation in the herring gull. – Behaviour (Suppl.) 17: 1–132.
Dwernychuk, L. W. and Boag, D. A. 1972. Ducks nesting in association with gulls – an ecological trap? – Can. J. Zool. 50: 559–563.
Eggers, S., Griesser, M., Nystrand, M. and Ekman, J. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. – Proc. R. Soc. B 273: 701–706.
Eggers, S., Griesser, M. and Ekman, J. 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. – Behav. Ecol. 19: 1056–1062.
Fontaine, J. J. and Martin, T. E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. – Ecol. Lett. 9: 428–434.
Forbes, L. S. 1989. Coloniality in herons: Lack's predation hypothesis reconsidered. – Colon. Waterbirds 12: 24–29.
Ghalambor, C. K. and Martin, T. E. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. – Anim. Behav. 60: 263–267.
Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E. and Jerde, C. L. 2006. Application of random effects to the study of resource selection by animals. – J. Anim. Ecol. 75: 887–898.
Götmark, F. and Andersson, M. 1984. Colonial breeding reduces nest predation in the common gull (*Larus canus*). – Anim. Behav. 32: 485–492.
Hatch, J. J. 1970. Predation and piracy by gulls at a ternery in Maine. – Auk 87: 244–254.
Hothem, R. L. and Hatch, D. 2004. Reproductive success of the black-crowned night-heron at Alcatraz Island, San Francisco Bay, California, 1990–2002. – Waterbirds 27: 112–125.
Hothem, R. L., Brussee, B. E. and Coates, P. S. 2013. Reproductive success of black-crowned night-herons and snowy egrets at Alcatraz Island, San Francisco Bay, California, 2012. Annual data summary. Prepared for Golden Gate National Recreation Area. – National Park Service.
Howell, J. A. and Pollak, T. 1991. Wildlife habitat analysis for Alcatraz Island, Golden Gate National Recreation Area, California. – In: Adams, L. W. and Leedy, D. L. (eds), Wildlife conservation in metropolitan environments. NIUW Symp. Ser. 2, pp. 157–164.
Kelly, J. P., Pratt, H. M. and Greene, P. L. 1993. The distribution, reproductive success, and habitat characteristics of heron and egret breeding colonies in the San Francisco Bay area. – Colon. Waterbirds 16: 18–27.
Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. – Biol. Rev. 84: 485–513.
Londoño, G. A., Levey, D. J. and Robinson, S. K. 2008. Effects of temperature and food on incubation behavior of the northern mockingbird, *Mimus polyglottos*. – Anim. Behav. 76: 669–677.
Luginbuhl, J. M., Marzluff, J. M., Bradley, J. E., Raphael, M. G. and Varland, D. E. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. – J. Field Ornithol. 72: 556–572.
Martin, T. E. 1993. Nest predation and nest sites. – Bioscience 43: 523–532.
Martin, T. E., Scott, J. and Menge, C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. – Proc. R. Soc. B 267: 2287–2293.
Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.
Quinn, J. L. and Ueta, M. 2008. Protective nesting associations in birds. – Ibis 150: 146–167.
Rastogi, A. D., Zanette, L. and Clinchy, M. 2006. Food availability affects diurnal nest predation and adult antipredator behavior in song sparrows, *Melospiza melodia*. – Anim. Behav. 72: 933–940.
Saenz, B. L., Thayer, J. A., Sydeman, W. J. and Hatch, D. A. 2006. An urban success story: breeding seabirds on Alcatraz Island, California, 1990–2002. – Mar. Ornithol. 34: 43–49.
Smith, P. A. and Wilson, S. 2010. Intraseasonal patterns in shorebird nest survival are related to nest age and defence behavior. – Oecologia 163: 613–624.
Smith, P. A., Dauncey, S. A., Gilchrist, H. G. and Forbes, M. R. 2012. The influence of weather on shorebird incubation. – In: Ribic, C. A., Thompson III, F. R. and Pietz, P. J. (eds), Video surveillance of nesting birds. Stud. Avian Biol. Ser. 43. Univ. of California Press, pp. 89–104.
Tulp, I. and Schekkerman, H. 2006. Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. – J. Avian Biol. 37: 207–218.
Väänänen, V. M. 2000. Predation risk associated with nesting in gull colonies by two *Aythya* species: observations and an experimental test. – J. Avian Biol. 31: 31–35.
van Vessem, J. and Draulans, D. 1986. The adaptive significance of colonial breeding in the grey heron *Ardea cinerea*: inter- and intra-colony variability in breeding success. – Ornis Scand. 17: 356–362.
Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the sandwich tern (*Sterna s. sandvicencis* Lath.). – Behaviour (Suppl.) 20: 1–193.
Watmough, B. R. 1978. Observations on nocturnal feeding by night herons *Nycticorax nycticorax*. – Ibis 120: 356–358.
Wheelright, N. T., Lawler, J. J. and Weinstein, J. H. 1997. Nest-site selection in savannah sparrows: using gulls as scarecrows? – Anim. Behav. 53: 197–208.
Whitehouse, H. L. K. and Armstrong, E. A. 1953. Rhythms in the breeding behaviour of the European wren. – Behaviour 5: 261–288.
Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. – Am. Nat. 100: 687–690.
Wittenberger, J. F. and Hunt, G. L. Jr 1985. The adaptive significance of coloniality in birds. – In: Farner, D. S. and King, J. R. (eds), Avian biology. Vol. 8. Academic Press, pp. 1–78.
Yerkes, T. 1998. The influence of female age, body mass, and ambient conditions on redhead incubation constancy. – Condor 100: 62–68.
Young, A. D. and Titman, R. D. 1986. Costs and benefits to red-breasted mergansers nesting in tern and gull colonies. – Can. J. Zool. 64: 2339–2343.
Zanette, L. Y., White, A. F., Allen, M. C. and Clinchy, M. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. – Science 334: 1398–1401.
Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. – Springer.