



Nest survival is influenced by parental behaviour and heterospecifics in a mixed-species colony

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Studies of avian nest success often focus on examining influences of variation in environmental and seasonal factors. However, in-depth evaluations can also incorporate variation in individual incubation behaviour to further advance our understanding of avian reproductive ecology. We examined these relationships in colonially nesting Black-crowned Night-Herons *Nycticorax nycticorax* using intensive video-monitoring methods to quantify incubation behaviours. We modelled nest survival as a function of both extrinsic factors and incubation behaviours over a 3-year period (2010–12) on Alcatraz Island, USA. Model-averaged parameter estimates indicated that nest survival increased as a function of greater incubation constancy (% of time spent incubating eggs within a 24-h period), and average daily precipitation throughout the nesting stage. Common Ravens *Corvus corax* are the only known nest predator of Night-Herons on Alcatraz Island, as on many other coastal Pacific islands. We also investigated the effects of heterospecific nesting of California Gulls *Larus californicus* and Western Gulls *Larus occidentalis* in a mixed-species colony with Night-Herons, based on nesting proximity data collected over a 2-year period (2011–12). This second analysis indicated that, in addition to incubation behaviours, nesting heterospecifics are an important factor for explaining variation in Night-Heron nest survival. However, contrary to our original expectation, we found that Night-Herons experienced increased nest survival with increasing distance from gull colony boundaries. These results may apply to other areas with multiple colonial nesting species and similar predator communities and climatic patterns.

Keywords: Black-crowned Night-Heron, California Gull, incubation behaviour, *Larus*, *Nycticorax*, predation, weather, Western Gull.

Many environmental factors influence avian nest survival, including nest-site characteristics (Martin *et al.* 2000), predator communities (Martin 1993) and climatic conditions (Crick & Sparks 1999, Morrison & Bolger 2002, Rodríguez & Bustamante 2003). Nest survival also depends on factors that vary among individual birds, such as age of breeding adults, reproductive experience (Raveling 1981, Pyle *et al.* 1991) and nesting behaviour (Martin *et al.* 2000, Allen Smith *et al.* 2007). Nesting behaviours such as incubation constancy (INC), nest attentiveness and nest defence are complex and are often less studied predictors of

avian nest survival. Research that evaluates the relative contributions of environmental and behavioural factors to nest survival will strengthen our overall understanding of avian reproductive ecology.

We carried out an intensive multi-year study, including video-monitoring techniques, on the nesting ecology of Black-crowned Night-Herons *Nycticorax nycticorax* on Alcatraz Island, California, USA. The rationale for an intensive study included a need to investigate a significant decline in Night-Heron nest success on Alcatraz Island from 75% in 1990–95 to 63% in 1996–2002 (Hotham & Hatch 2004), and a further decline to 40% in 2003–09 (Hotham *et al.* 2011). We chose this colonial species and location because of a unique opportunity

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to evaluate correlates of variation in nest success based on extensive knowledge of nest predators, ease of access to nesting colonies, the presence of multiple colonial nesting species to evaluate effects of nesting heterospecifics, and extensive knowledge of historical nesting success based on > 20 years of monitoring Night-Heron populations at this study site (Hothem *et al.* 2011).

Predation has been identified as a primary cause of nest failure for Night-Herons (Blus *et al.* 1997, Hothem & Hatch 2004), and the effects of various factors contributing to nest predation are likely to be dependent on the ecology of both the prey species and predator communities (Allen Smith *et al.* 2007). Common Ravens *Corvus corax* are efficient egg predators and can cause significant damage in heron colonies (Kelly *et al.* 2005). Ravens are territorial (Avery *et al.* 1995) and have been considered an important predator of Night-Heron nests on Alcatraz Island over the past decade (Hothem & Hatch 2004). Several studies have indicated that birds can alter their nesting behaviour in response to perceived predation risk. For example, when perceived risk is higher, birds reduce trips to provision nests, thereby minimizing activity at the nest-site (Ghalambor & Martin 2000). Conversely, birds display higher parental investment (e.g. increased egg size) when perceived risk is lower (Fontaine & Martin 2006). The ability of parent birds to perceive predation risk and adapt parental behaviour accordingly is a likely determinant of reproductive success, although few studies of avian nest survival incorporate incubation behaviour.

An additional adaptation for increased reproductive success is the selection of advantageous nest-site characteristics (Martin & Roper 1988, Martin *et al.* 2000), such as sites with favourable placement within a colony (Burger 1981, Brunton 1997). Some birds nest in association with more territorial species to gain a protective advantage (Wiklund 1982, Quinn & Ueta 2008). On Alcatraz Island, Night-Herons are often found nesting in mixed-species colonies with both Western Gulls *Larus occidentalis* and California Gulls *Larus californicus*. Both gull species are highly territorial, especially during the breeding season (Hunt & Hunt 1975). Because Night-Herons exhibit little or no predator mobbing or other nest defence behaviours, nesting in these mixed-species colonies may offer some protection. However, both gull species are also egg predators (Pierotti & Annett 1995, Winkler 1996), and could reduce nest suc-

cess for those Night-Herons nesting close to active gull nesting areas.

We designed this study to evaluate multiple *a priori* expectations regarding the effects of incubation behaviours and nest proximity to nesting gulls on Night-Heron nest survival, while also accounting for weather conditions and seasonal factors. We first predicted that variation in nest survival would be explained by incubation behaviour. Specifically, we predicted greater nest survival for Night-Herons that exhibited higher INC, as these birds would be less likely to draw attention from visually cued predators, such as Ravens. We also predicted that any effect of incubation behaviour on nest survival would be most influential during times of peak predation pressure, specifically daylight hours when Ravens are hunting. We also predicted that variation in nest survival would be explained by Night-Heron nest proximity to nesting gulls. We predicted that the territorial nature of gulls would provide more benefit than harm to nearby nesting Night-Herons, in support of protective relationships of nesting birds that have been observed elsewhere (Quinn & Ueta 2008). Our study area is likely to be typical of other Pacific Coast islands with no evidence of mammalian predators and consisting of a relatively isolated ecosystem containing multiple colonial nesting species. Therefore, our results may apply to other island systems with mixed-species colonies in similar geophysical settings.

METHODS

Study area

Alcatraz Island (37.8°N, 122.4°W) is a 9.1-ha island located in San Francisco Bay approximately 1.6 km north of the city of San Francisco, California (Fig. 1). Originally a harbour-defence fort after the Civil War (1847–1907), then a military prison (1907–33), Alcatraz was used as a federal penitentiary (1933–63) before being designated as public lands (1963–71) and subsequently opened as the first unit of the Golden Gate National Recreation Area (Thompson 1979, Martini 1990).

The National Parks Service began managing the island in 1973 (Howell & Pollak 1991). The island is occupied by mostly non-native plant species and consists of many historic buildings, cement roads and piles of rubble from demolished buildings. Historically, Victorian-era gardens and lawns, as well as large specimen shrubs and trees, were

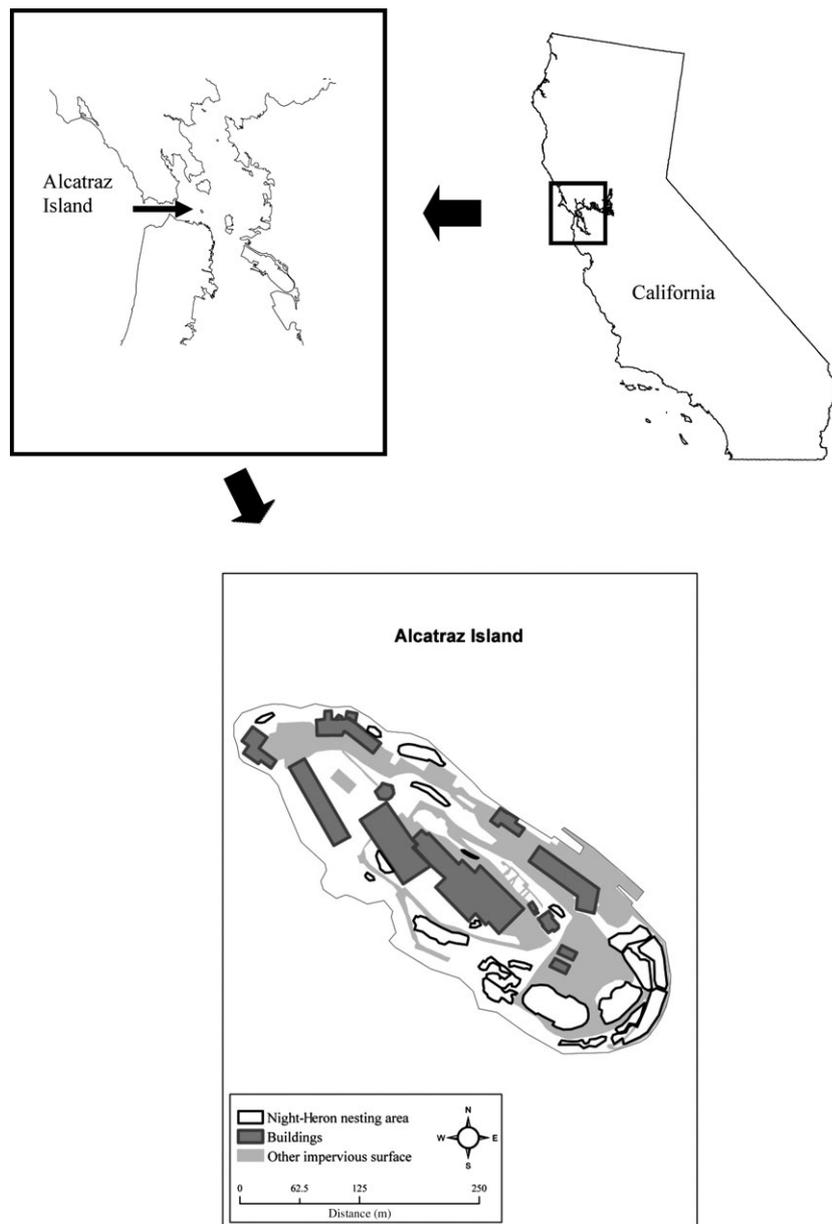


Figure 1. Map of Black-crowned Night-Heron nesting areas on Alcatraz Island during 2010–12.

planted to create a more hospitable place to live (Martini 1990). These include agave *Agave* spp., aloe *Aloe* spp., Mirror Plant *Coprosma repens*, rose *Rosa* spp., fuchsia *Fuchsia* spp., English Ivy *Hedera helix*, ice plant *Carpobrotus* spp., eucalyptus *Eucalyptus* spp., Cypress *Cupressus macrocarpa* and numerous other species.

Alcatraz was uninhabited from 1963 to 1969, during which time garden areas naturalized and spread, and nesting birds began to re-colonize,

including Night-Herons in 1975 (Bradley 2005). Today, the island provides nesting grounds for colonies of several bird species including Night-Herons, Snowy Egrets *Egretta thula*, Western Gulls, California Gulls, and both Brandt's Cormorant *Phalacrocorax penicillatus* and Pelagic Cormorant *Phalacrocorax pelagicus*. Other non-colonial species, such as Pigeon Guillemots *Cepphus columba*, Black Oystercatchers *Haematopus bachmani* and Ravens, also nest on the island.

Average temperatures during the breeding season range from 4 to 16 °C at the beginning of March to 12 to 20 °C in July. For San Francisco Bay, most annual precipitation occurs from January to March. Precipitation during the breeding season averages 9.1 cm in March but < 0.5 cm in June and July.

Nest monitoring

We conducted intensive weekly censuses from mid-April to late July of 2010–12 to locate and mark Night-Heron nests during either the laying period or the initial stages of incubation. While nest detectability on the island is likely to vary depending on surrounding vegetation, we conducted repeated intensive searches so as not to miss nests even in dense vegetation. In addition, detectability of nests was enhanced by our knowledge of historical nesting areas of Night-Herons. On Alcatraz, Night-Heron nests average *c.* 1.1 m off the ground and are usually in small trees and shrubs, but have also been found in rubble piles (Hothem *et al.* 2010). Nest searches were conducted within each previously identified Night-Heron nesting area, and new nests were added to the count each week during the breeding season. All nests were revisited weekly and classified as successful (at least one egg hatched), predated, partially predated or abandoned during the egg stage. At each nest-site, we recorded co-ordinates using a hand-held global positioning system (Universal Transverse Mercator (UTM), North American Datum 1983).

Behavioural and environmental variables

To measure incubation behaviours, we used digital video recorders (DVRs; continuous recordings of 24 h/day) and micro-cameras; the latter at a stratified sample of Night-Heron nests selected to maximize the amount of incubation data and also to proportionally represent used habitat types. Micro-cameras (30 × 110 mm with a 3.6-mm lens; EZ Spy Cam; Los Angeles, CA, USA) were mounted 0.5–1.0 m from nests on nearby vegetation or attached to a camouflaged iron stake. Each camera included seven infrared (950 nm wavelength) light-emitting diodes, a wavelength invisible to vertebrates, allowing us to capture images both during the day and at night. Cameras and cables

were concealed using camouflage duct tape and vegetation. Cables extended up to 100 m to a four-channel H.264 DVR system (AV Tech Corp., Hong Kong, China) housed in a camouflaged casing and hidden under vegetation or beneath burlap. To maximize data collection, we set DVRs to record continuously at the lowest frame per second (fps) setting (7 fps in 2010 and 2011, and 15 fps in 2012). The status of each nest was checked by observers in the field using a hand-held video monitor (18-cm-wide screen) during weekly island visits. Cameras were maintained on each monitored nest until the nest failed or the eggs hatched.

We viewed a random sample of nesting calendar days (1–10 calendar days per nest, depending on how long the nest was active following camera installation), and defined INC as the total time of physical contact between the parent bird and the eggs. Within each selected day, we randomly chose two 10-min intervals per hour. Random subsampling of this kind was deemed appropriate based on evidence that similar techniques are an efficient way to estimate incubation behaviours (Davis & Holmes 2012). To eliminate potential effects of disturbance on behaviour caused by observers, we excluded dates on which island-wide nest identification and monitoring occurred. Nests that had cameras for less than one full day before nest failure or nest hatch were also excluded. We calculated the average daily percentage INC per individual nest. Data on temperature and precipitation (US National Climate Data Center, Asheville, NC, USA) were obtained from a San Francisco-based weather station (Weather Station 23272, 37.7°N, 122.4°W) and compiled for each nest based on the duration of incubation.

In the weeks of 7 and 14 June 2011 and 7 May 2012, we located gull nests. All locations were marked on printed paper maps and later transferred to a geographic information system (GIS). We created two distance measures to describe relationships between nesting Night-Herons and gulls. First, we estimated gull colony boundaries by employing a kernel density estimator on gull nest location data with a smoothing parameter estimated with a least squares cross-validation technique (Hall 1983, Worton 1989) using geospatial modelling environment (Beyer 2012). We then derived an isopleth (contour) that contained 50% of the probability density function, which appropriately represented the core density of gulls and

approximated a core boundary. The second measure was the distance from each Night-Heron nest to the nearest gull nest. Both measures were created using SPATIAL ANALYST tools (ARCGIS 10.1 and ESRI 2012, Redlands, CA, USA).

Modelling nest survival

For all nests, we recorded an encounter history including the date that each nest was found, the date it was last checked and the date of nest fate (predated, abandoned or hatched). A nest was considered successful if at least one egg survived to hatching. We estimated daily survival probability (DSP) using generalized linear models (specified binomial error distribution and logit link function) in the program R with the package RMARK (R version 3.0.1; Laake & Rexstad 2007), which implements the program MARK ('nest survival model'; White & Burnham 1999). Using DSP, we derived cumulative survival probability (nest initiation to hatching of the first egg at 25 days; Hothem *et al.* 2010) and 95% confidence intervals (CIs) using the delta method (Powell 2007). To estimate the effects of camera presence on nest survival, we assigned a group-level covariate for two discrete categories of camera (present or absent) at each nest-site. For video-monitored nests only, we coupled encounter histories with multiple explanatory covariates (Table 1; program MARK; White & Burnham 1999), and carried out nest survival modelling using two separate analyses. The first analysis used data from the full duration of the study (2010–12;

Table 1. Explanatory variables used to develop survival models for Black-crowned Night-Heron nests on Alcatraz Island, 2010–12.

Group	Model	Description
Year	YEAR	2010, 2011, 2012
Temporal	INIT	Ordinal date of nest initiation
Weather	TMAX	Maximum temperature (°C) experienced over incubation period
	PRCP	Average precipitation (mm) over incubation period
Behaviours	INC	Incubation constancy (%): time adult brood patch is in contact with eggs
Heterospecifics ^a	DISTNN	Distance (m) to nearest gull nest
	DIST50	Distance (m) to 50% gull colony boundary

^aGull metrics were only measured in 2011 and 2012.

hereafter referred to as 'complete video dataset'), and considered year, nest initiation date, average precipitation (PRCP; mm), maximum temperature (TMAX; °C) and INC as individual covariates in the survival analyses (Table 1). The initiation date covariate was included to account for seasonal effects on nest survival. We then conducted a second analysis using all variables with unconditional CIs that did not overlap zero. This used data collected during 2011 and 2012 (hereafter referred to as the 'restricted dataset'), which included distance to the nearest gull neighbour (m) and distance to the 50% gull colony boundary (m).

For both analyses, we included all possible additive covariate combinations. We used Akaike's information criterion (AIC) corrected for sample size (c) and calculated differences in AIC_c values (Δ) and Akaike weights (w_i ; Anderson 2008) to compare across models and evaluate evidence. We then calculated model-averaged parameter estimates (β) and unconditional CIs (Anderson 2008) for each covariate. Because correlated predictor variables can result in misleading parameter estimates when using model-averaging techniques (Cade 2015), we excluded models with covariates that co-varied ($R \geq |0.65|$) to reduce the effects of multicollinearity (Dormann *et al.* 2013).

We further investigated the effect of time of day on any relationship between INC and nest survival. To do this, we divided each day into three equal daylight periods (early light (EL), mid-light (ML) and late light (LL)), and three equal dark periods (early dark (ED), mid-dark (MD) and late dark (LD)), and calculated average INC for each nest for each of the six light periods. We then modelled DSP as a function of INC for each of these six periods separately, and we evaluated the results using information-theoretic criteria as described previously across the model set.

RESULTS

We found 330 Night-Heron nests that were active for more than 1 day and could be included in analyses ($n = 134$ in 2010; $n = 115$ in 2011; $n = 81$ in 2012). Nesting substrates included blackberry *Rubus* spp., fuchsia, English Ivy, the shrubby, evergreen tree *Pittosporum crassifolium*, the Century Plant *Agave americana* and rubble piles from demolished buildings. The cumulative nest survival probability over the 25-day incubation period was 0.341 (95% CI = 0.285–0.399).

Of 330 nests, 51% were successful and 49% failed. Based on nest remains, we were unable reliably to classify causes of failure for nests without video cameras. We installed video cameras on 100 nests ($n = 19$ in 2010; $n = 38$ in 2011; $n = 43$ in 2012), with a survival probability of 0.544 (95% CI = 0.427–0.648%). Of 100 video-monitored nests, 60% successfully hatched ($n = 12$ in 2010; $n = 19$ in 2011; $n = 29$ in 2012), 21% were abandoned ($n = 1$ in 2010; $n = 9$ in 2011; $n = 11$ in 2012 (including 10 nests abandoned just prior to or at camera installation)), 10% were predated by Ravens ($n = 5$ in 2010; $n = 5$ in 2011; $n = 0$ in 2012), 5% failed to hatch ($n = 0$ in 2010; $n = 4$ in 2011; $n = 1$ in 2012) and 4% were predated by Night-Herons ($n = 1$ in 2010; $n = 1$ in 2011; $n = 2$ in 2012).

Survival models: complete dataset

We obtained behaviour data for 80 video-monitored nests from 2010 to 2012 (17 in 2010, 29 in 2011 and 34 in 2012), excluding those that hatched or failed within 24 h of camera installation. We found no evidence of correlation among predictor variables that would result in multicollinearity effects in models using the complete dataset given the exclusion criterion (Table S1). The model set from the complete video dataset consisted of 32 models. The most parsimonious model included a negative effect of initiation date and positive effects of TMAX, PRCP and INC

($w = 0.17$; Table 2). Seven models had $\Delta AIC < 2$ from the best model, all of which included INC.

Model-averaged parameter estimates indicated that both PRCP and INC were important variables for describing nest survival in the complete video dataset; the unconditional CIs averaged across all models containing these covariates did not overlap zero. However, CIs for PRCP overlapped zero in eight of 16 models, whereas CIs for INC did not overlap zero in any model in which that covariate occurred (Table 3). Model-averaged parameter estimates indicated that, for every 1% increase in INC, the odds of daily nest survival increased by 8.5% (95% CI = 3.5–13.6%; Fig. 2), and nests that experienced twice the daily average PRCP (average \pm se = 0.50 ± 0.07 mm) had a 3.4 times greater odds of daily survival (95% CI = 1.0–11.6; Fig. 3).

Survival models: restricted dataset

Sixty-three nests were used in the restricted dataset to evaluate the survival of video-monitored nests during 2011–12. Based on the exclusion criterion, we found no evidence of correlation between any of the predictor variables that would result in models with multicollinearity effects using the restricted dataset (Table S2). The model set from the restricted dataset comprised 16 models. The most parsimonious model using the restricted dataset included positive effects of PRCP, INC and distance to the 50% gull colony boundary

Table 2. Model selection of nest survival models for Black-crowned Night-Heron nests on Alcatraz Island, 2010–12.

Dataset ^a	Explanatory variables ^b	<i>K</i>	$-2\ln L^c$	ΔAIC_c	<i>w</i>
Complete	INIT + TMAX + PRCP + INC	5	118.61	0.00	0.17
	YEAR + TMAX + PRCP + INC	6	116.66	0.07	0.16
	YEAR + INIT + TMAX + PRCP + INC	7	114.85	0.28	0.15
	YEAR + PRCP + INC	5	119.56	0.94	0.11
	TMAX + PRCP + INC	4	122.28	1.65	0.07
	INIT + TMAX + INC	4	122.46	1.83	0.07
	YEAR + INIT + PRCP + INC	6	118.43	1.83	0.07
Restricted	PRCP + INC + DIST50	4	91.37	0.00	0.48
	PRCP + INC + DISTNN + DIST50	5	91.30	1.95	0.18

^aThe complete dataset consisted of nests from the full duration of the study ($n = 80$; 2010–12), while the restricted dataset consisted of a subset of the data ($n = 63$; 2011–12) which included additional environmental factors associated with gulls. ^bINIT, initiation date; TMAX, maximum temperature; PRCP, precipitation; INC, incubation constancy; DIST50, distance to the 50% gull colony boundary; DISTNN, distance to the nearest gull neighbour. ^c $-2\ln L$ for the null model was 139.02 for the complete dataset and 110.06 for the restricted dataset. Column abbreviations: $-2\ln L$, $-2\log(\text{likelihood})$; *K*, number of estimated parameters; AIC_c , Akaike's information criterion with second-order bias correction; ΔAIC_c , difference (Δ) in AIC_c between most parsimonious model and model of interest; *w*, model probability.

Table 3. Model-averaged parameter estimates with unconditional confidence intervals (CIs) from nest survival models for Black-crowned Night-Heron nests on Alcatraz Island, 2010–12.

Dataset ^a	Explanatory variables ^b	Number of models	w	Model-averaged parameter estimate	Unconditional 95% CI	Number of models 95% CIs overlap zero
Complete	INC	16	0.97	0.08	0.05	0
	PRCP	16	0.81	1.23	1.22	8
	TMAX	16	0.67	0.12	0.13	11
	INIT	16	0.59	-0.02	0.03	10
	YEAR	16	0.53	NA	NA	16
Restricted	DIST50	8	0.97	0.07	0.06	0
	INC	8	0.83	0.06	0.05	0
	PRCP	8	0.80	1.10	1.19	8
	DISTNN	8	0.28	-0.02	0.18	8

^aThe complete dataset consisted of nests from the full duration of the study ($n = 80$; 2010–12), while the restricted dataset consisted of a subset of the data ($n = 63$; 2011–12) which included additional environmental factors associated with gulls. ^bINIT, initiation date; TMAX, maximum temperature; PRCP, precipitation; INC, incubation constancy; DIST50, distance to the 50% gull colony boundary; DISTNN, distance to the nearest gull neighbour.

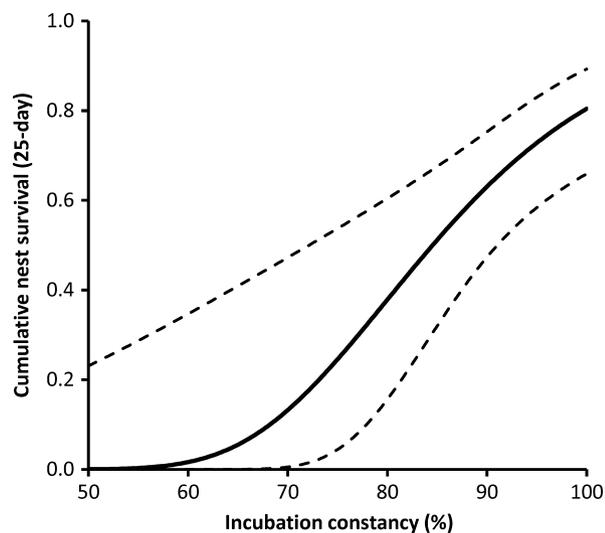


Figure 2. The estimated effect of incubation constancy on nest survival of Black-crowned Night-Herons nesting on Alcatraz Island in 2010–12. Predicted values were derived from the single-variable model using the complete dataset. Dotted lines represent 95% confidence intervals.

(DIST50; $w = 0.48$; Table 2). Although the top two models included the PRCP covariate, the CIs overlapped zero in every model in which the covariate occurred (Table 3). Model-averaged parameter estimates revealed that INC and DIST50 were important variables for describing nest survival in the restricted dataset; the unconditional CIs of these variables did not overlap zero. In fact, CIs for these covariates did not overlap zero in any model in which they occurred

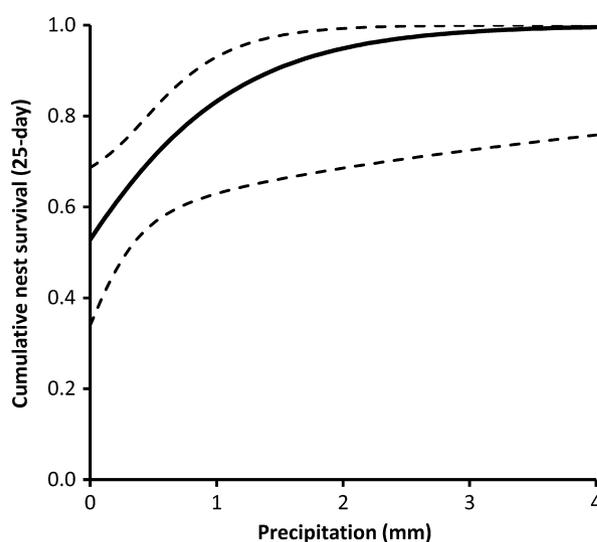


Figure 3. The estimated effect of precipitation (mm) on nest survival of Black-crowned Night-Herons nesting on Alcatraz Island in 2010–12. Predicted values were derived from the single-variable model using the complete dataset. Dotted lines represent 95% confidence intervals.

(Table 3). Model-averaged parameter estimates indicate a 6.6% (95% CI = 1.5–11.9) increase in the odds of daily nest survival for every 1% increase in INC. The results also indicate that the inclusion of heterospecific covariates explained additional variation in Night-Heron nesting survival. For every 1-m increase in distance from the 50% gull colony boundary, the odds of daily nest survival increased by 7.3% (95% CI = 1.2–13.8; Fig. 4).

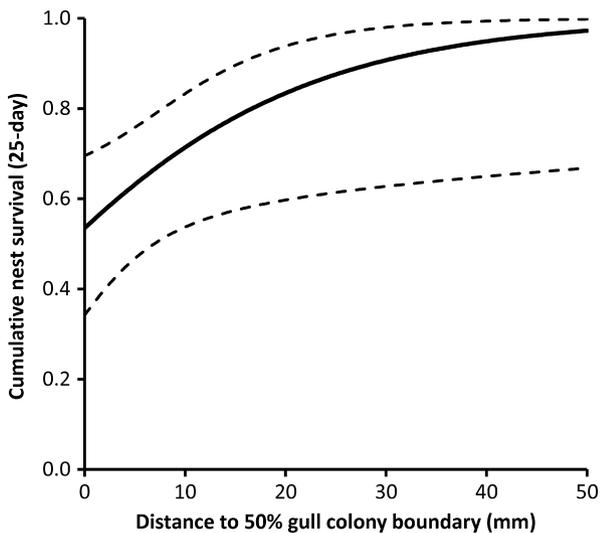


Figure 4. The estimated effect of gull colony boundary on nest survival of Black-crowned Night-Herons nesting on Alcatraz Island in 2011–12. Predicted values were derived from the single-variable model using the restricted dataset. Dotted lines represent 95% confidence intervals.

Post hoc analysis: light period and incubation constancy

INC during the early dark period (INC ED; $w_{\text{INC ED}} = 0.62$) was 3.2 times more likely to be included in the best model explaining variation in nest survival than overall average INC ($w_{\text{INC}} = 0.19$; Table 4). We found that those birds that exhibited the lowest INC, especially during the early dark hours, were most likely to fail (Fig. 5). Specifically, nests that failed exhibited 88.8% (95% CI = 81.8–95.8%) average INC in early dark hours, whereas successful nests averaged 98.1% (95% CI = 97.8–98.4%).

DISCUSSION

In this study, we identified clear and predictable relationships between incubation behaviour of Night-Heron parents and the success of their nests, while accounting for other factors that contribute to nest survival. While increased nest attentiveness can reduce a nest's vulnerability to predation (Rastogi *et al.* 2006), INC is also an indicator of parental investment in a nesting attempt, which is mediated hormonally in the parent bird (Hall 1987). For example, contact between the adult's brood patch and eggs stimulates production of the hormone prolactin, which is responsible for the

Table 4. Model selection of nest survival models for Black-crowned Night-Heron nests on Alcatraz Island, 2010–12, with incubation constancy (INC) by light period (ED, early dark; MD, mid-dark; LD, late dark; EL, early light; ML, mid-light; LL, late light).

Explanatory variable	K	$-2\ln L$	ΔAIC_c	w
INC ED	2	127.12	0.00	0.62
INC	2	129.45	2.33	0.19
INC MD	2	130.20	3.08	0.13
INC LD	2	132.30	5.18	0.05
INC EL	2	136.70	9.58	0.01
Null	1	139.02	9.89	0.00
INC ML	2	138.37	11.25	0.00
INC LL	2	138.63	11.50	0.00

Column abbreviations: $-2\ln L$, $-2\log(\text{likelihood})$; K , number of estimated parameters; AIC_c , Akaike's information criterion with second-order bias correction; ΔAIC_c , difference (Δ) in AIC_c between best approximating model and model of interest; w , model probability.

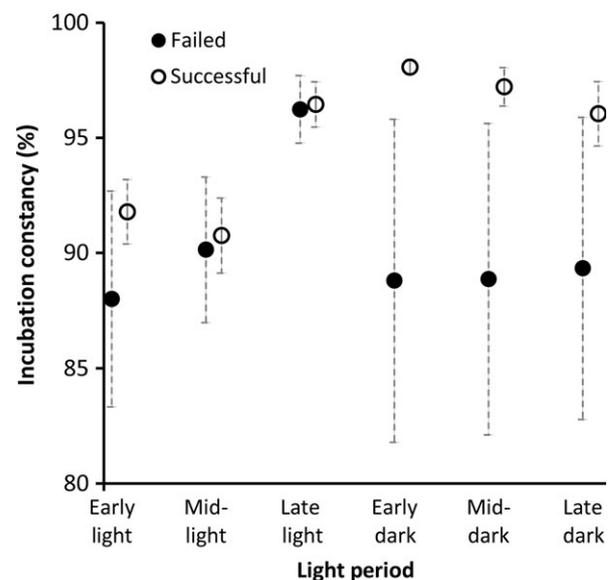


Figure 5. Comparison of incubation constancy by light period between successful and failed nests of Black-crowned Night-Herons on Alcatraz Island in 2010–12. Dotted lines represent 95% confidence intervals.

expression of parental investment in a reproductive attempt (Angelier & Chastel 2009). Birds that invest less in their nests may be more likely to abandon, or to respond to a predator by fleeing, which leaves their nest unguarded and may signal the presence of the nest to a predator.

With the use of video-monitoring, we were able to confirm that the main predator of Night-Heron

nests on Alcatraz is the Common Raven, a visually cued predator. However, Ravens only started nesting on Alcatraz in the mid-1990s, probably contributing to long-term decreases in Night-Heron nest survival. Given that Ravens hunt using visual cues, we originally predicted that Night-Herons that exhibited riskier behaviours (i.e. lower INC) during the times of greatest predator activity (i.e. daylight) would be most likely to fail, largely because those risky behaviours would cue the predator to the location of the nest (Skutch 1949). However, we found that failed nests were more closely associated with lower INC at night. Night-Herons are primarily nocturnal or crepuscular foragers (Watmough 1978), but during the breeding season they have been found to shift their time budgets, sometimes becoming active over the entire 24-h day (Fasola 1984). In fact, in a concurrent study of time budgets of Night-Herons on Alcatraz, we found that, generally, Night-Herons were most active during the early- and mid-light periods, and were inactive during the night (Coates *et al.* 2015). Birds with low INC at night are probably foraging or exhibiting other self-maintenance behaviours (e.g. preening) to satisfy their own energetic requirements. Lower INC might also be indicative of birds that require more time to acquire sufficient nutrients for both their own and their nest's survival, such as inexperienced nesters or breeding birds that have lost a mate.

Our original expectation predicted that gulls protected Night-Herons against predation by Ravens. Gulls offer protection from avian predation to a variety of nesting species, such as grebes (Burger 1984), Savannah Sparrows *Passerculus sandwichensis* (Wheelright *et al.* 1997) and several duck species (Dwernychuk & Boag 1972, Young & Titman 1986, Väänänen 2000). However, our results indicate that Night-Herons nesting further from the core colony boundary of gulls were more likely to be successful than those nesting closer to gulls. We did not observe gulls preying on Night-Heron nests on any of the video-monitored nests, and we have no evidence that gulls would be deterred from depredating a nest because of the presence of a camera on the nest (Herring *et al.* 2011). Therefore, the effect of gulls on Night-Heron nest success may be indirect. For example, by nesting near a territorial species, adult Night-Herons may be subjected to mobbing behaviours by gulls, and the territoriality of the gulls may affect the adult Night-Heron's ability to move

freely to and from the nest, especially where gull nest density is the greatest. This may result in higher nest abandonment rates and thus lower survival rates which outweigh any protective effect, although this possibility remains to be tested.

Although effects of weather were not the main focus of this study, our results indicated that increased rainfall was associated with higher nest survival rates of Night-Herons. However, this relationship did not persist within the restricted dataset. The lack of an effect of precipitation within the restricted dataset could indicate a weak relationship resulting from episodic precipitation events, whereby those birds that survived would be more likely to encounter precipitation. Alternatively, the lack of weather effects within the restricted data may be explained by the reduction in sample size and, thus, statistical power in the analysis. In fact, we found similar effects in the complete and restricted datasets, but with wider CIs in the latter, suggesting this to be the case.

Video-monitoring revealed that nest failure resulted from both predation and abandonment. Predation was the main cause of nest failure only during 2010, a year when Ravens successfully hatched young on the island. Ravens have been identified as the only interspecific predator on Night-Heron nests at our study area based on video-monitoring, accounting for 100% of interspecific nest predations. We found no evidence of Ravens successfully nesting on Alcatraz Island in 2011 and 2012, and in these years the main cause of nest failure was abandonment.

Nest survival rates were higher at nests with cameras than in the full sample. It is possible that cameras act as a deterrent to potential predators but we do not believe this to be the case based on other studies using similar video-monitoring techniques (King *et al.* 2001, Coates *et al.* 2008). More probably, the effect is explained by the timing of our sampling efforts. Specifically, cameras were installed at nests on average 12 days after nest initiation. Although we did not specifically consider nest age in our survival models, studies have found that nests are more likely to be predated or abandoned in the early stages of incubation (Klett & Johnson 1982, Dinsmore *et al.* 2002) during which time we had fewer nests with cameras than at later stages of incubation.

We did not consider the effect of parental age on nest survival in this study because, although second- and third-year birds are identifiable by

their plumage, we did not observe any of these younger birds on our video-monitored nests. Additionally, we were unable to include food availability in the analysis, which is often difficult to assess, especially for species such as Night-Herons which are opportunistic generalists, not specializing in one prey type (Hothem *et al.* 2010). Lastly, the video-monitored sample sizes did not permit us to differentiate factors that influence nest predation rates from those that influence abandonment rates. Future research exploring how such factors might contribute additively to nest abandonment and predation rates, with additional information regarding food availability and age and experience of the breeding adults, would contribute greatly to the reproductive ecology of colonial nesting birds.

In summary, we found clear relationships between nest survival of a colonial nesting species and factors related to nesting behaviour and proximity to nesting heterospecifics. Specifically, we found that INC greatly influenced nest survival and that nest-site location in relation to gull colonies plays an important role in Night-Heron nest survival. This research helps to elucidate the causes of long-term decreases in Night-Heron nest survival on Alcatraz. For example, in addition to confirming the effects of Raven predation on Night-Heron nest survival, we now understand that growing numbers of nesting gulls may have contributed to reduced nest survival probabilities since the mid-1990s. Since 1990, Western Gull numbers on Alcatraz have increased from *c.* 500 nests to > 1000 nests in 2008 (Hothem *et al.* 2011). As gull colony boundaries expand closer to Night-Heron nesting areas, this indirectly influences Night-Heron nest survival. This research warrants further investigation of the effects of nesting gulls on Night-Heron fledgling survival to understand how mixed-species colony nesting influences overall reproductive success. Our results reveal mechanistic relationships between nest survival, environment and incubation behaviour of a colonially nesting species on Alcatraz Island and may have relevance for other areas with similar environmental characteristics and climatic patterns.

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REFERENCES

- Allen Smith, P., Gilchrist, H.G. & Smith, J.N.M. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. *Condor* **109**: 15–31.
- Anderson, D.R. 2008. *Model Based Inferences in the Life Sciences*. New York: Springer.
- Angelier, F. & Chastel, O. 2009. Stress, prolactin and parental investment in birds: a review. *Gen. Comp. Endocrinol.* **163**: 142–148.
- Avery, M.L., Pavelka, M.A., Bergman, D.L., Decker, D.G., Knittle, C.E. & Linz, G.M. 1995. Aversive conditioning to reduce raven predation on California Least Tern eggs. *Colon. Waterbirds* **18**: 131–138.
- Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.6.0.0). Available at: <http://www.spatial ecology.com/gme> (accessed 4 January 2013).
- Blus, L.J., Rattner, B.A., Melacon, M.J. & Henny, C.J. 1997. Reproduction of Black-crowned Night-Herons related to predation and contaminants in Oregon and Washington, USA. *Colon. Waterbirds* **20**: 185–197.
- Bradley, D. 2005. *Cultural Landscapes Inventory: Alcatraz Island*. San Francisco, CA: National Park Service.
- Brunton, D.H. 1997. Impacts of predators: center nests are less successful than edge nests in a large nesting colony of Least Terns. *Condor* **99**: 372–380.
- Burger, J. 1981. A model for the evolution of mixed-species colonies of Ciconiiformes. *Q. Rev. Biol.* **56**: 143–167.
- Burger, J. 1984. Grebes nesting in gull colonies: protective associations and early warning. *Am. Nat.* **123**: 327–337.
- Cade, B.S. 2015. Model averaging and muddled multimodel inferences. *Ecology* **96**: 2370–2382.
- Coates, P.S., Connelly, J.W. & Delehanty, D.J. 2008. Predators of Greater Sage-Grouse nests identified by video monitoring. *J. Field Ornithol.* **79**: 421–428.
- Coates, P.S., Brussee, B.B., Hothem, R.L., Howe, K.H., Casazza, M.L. & Eadie, J.M. 2015. The effects of heterospecifics and climatic conditions on incubation behavior within a mixed-species colony. *J. Avian Biol.* **46**: 1–10.
- Crick, H.Q.P. & Sparks, T.H. 1999. Climate change related to egg-laying trends. *Nature* **399**: 423–424.
- Davis, S.K. & Holmes, T.G. 2012. Sprague's Pipit incubation behavior. In Ribic, C.A., Thompson, F.R. 3rd & Pietz, P.J. (eds) *Video Surveillance of Nesting Birds. Studies in Avian Biology (No. 43)*: 67–76. Berkeley, CA: University of California Press.
- Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**: 3476–3488.

- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Márquez, J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**: 27–46.
- Dwernychuk, L.W. & Boag, D.A. 1972. Ducks nesting in association with gulls—an ecological trap? *Can. J. Zool.* **50**: 559–563.
- Fasola, M. 1984. Activity rhythm and feeding success of nesting night herons *Nycticorax nycticorax*. *Ardea* **72**: 217–222.
- Fontaine, J.J. & Martin, T.E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**: 428–434.
- Ghalambor, C.K. & 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.
- Hall, P. 1983. Large sample optimality of least squares cross-validation in density estimation. *Ann. Stat.* **11**: 1156–1174.
- Hall, M.R. 1987. External stimuli affecting incubation behavior and prolactin secretion in the duck (*Anas platyrhynchos*). *Horm. Behav.* **21**: 269–287.
- Herring, G., Ackerman, J.T., Takekawa, J.Y., Eagles-Smith, C.A. & Eadie, J.M. 2011. Identifying nest predators of American Avocets (*Recurvirostra americana*) and Black-necked Stilts (*Himantopus mexicanus*) in San Francisco Bay, California. *Southwest. Nat.* **56**: 35–43.
- Hothem, R.L. & 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. & Davis, W.E.Jr. 2010. Black-crowned night-heron (*Nycticorax nycticorax*). In Poole, A. (ed.) *The Birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/074>.
- Hothem, R.L., Brussee, B.E. & Coates, P.S. 2011. *Reproductive success of Black-crowned Night-Herons and Snowy Egrets at Alcatraz Island, San Francisco Bay, California, 2010. Annual Data Summary*. San Francisco, CA: National Park Service.
- Howell, J.A. & Pollak, T. 1991. Wildlife habitat analysis for Alcatraz Island, Golden Gate National Recreation Area, California. In Adams, L.W. & Leedy, D.L. (eds) *Wildlife Conservation in Metropolitan Environments (NIUW Symposium Series 2)*: 157–164. Columbia, MD: National Institute for Urban Wildlife.
- Hunt, G.L. & Hunt, M.W. 1975. Reproductive ecology of the Western Gull: the importance of nest spacing. *Auk* **92**: 270–279.
- Kelly, J.P., Etienne, K.L. & Roth, J.E. 2005. Factors influencing the nest predatory behaviors of common ravens in heronries. *Condor* **107**: 402–415.
- King, D.I., DeGraaf, R.M., Champlin, P.J. & Champlin, T.B. 2001. A new method for wireless video monitoring of bird nests. *Wildl. Soc. Bull.* **29**: 349–353.
- Klett, A.T. & Johnson, D.H. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* **99**: 77–87.
- Laake, J. & Rexstad, E. 2007. RMark—an alternative approach to building linear models. In Cooch, E. & White, G. (eds). *Program MARK: A Gentle Introduction: Appendix C*. <http://www.phidot.org/software/mark/docs/book/>.
- Martin, T.E. 1993. Nest predation and nest sites. *Bioscience* **43**: 523–532.
- Martin, T.E. & Roper, J.J. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* **90**: 51–57.
- Martin, T.E., Scott, J. & Menge, C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. B* **267**: 2287–2293.
- Martini, J.A. 1990. *Fortress Alcatraz. Guardian of the Golden Gate*. Kailua, HI: Pacific Monograph.
- Morrison, S.A. & Bolger, D.T. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia* **133**: 315–324.
- Pierotti, R.J. & Annett, C.A. 1995. Western Gull (*Larus occidentalis*). In Poole, A. (ed.) *The Birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/174>.
- Powell, L.A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *Condor* **109**: 949–954.
- Pyle, P., Spear, L.B., Sydeman, W.J. & Ainley, D.G. 1991. The effects of experience and age on the breeding performance of Western Gulls. *Auk* **108**: 25–33.
- Quinn, J.L. & Ueta, M. 2008. Protective nesting associations in birds. *Ibis* **150**: 146–167.
- Rastogi, A.D., Zanette, L. & Clinchy, M. 2006. Food availability affects diurnal nest predation and adult antipredator behavior in Song Sparrows, *Melospiza melodia*. *Anim. Behav.* **72**: 933–940.
- Raveling, D.G. 1981. Survival, experience, and age in relation to breeding success of Canada Geese. *J. Wildl. Manag.* **45**: 817–829.
- Rodríguez, C. & Bustamante, J. 2003. The effect of weather on Lesser Kestrel breeding success: can climate change explain historical population declines? *J. Anim. Ecol.* **72**: 793–810.
- Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* **91**: 430–455.
- Thompson, E.N. 1979. *The Rock, a Natural History of Alcatraz Island, 1847–1972*. Denver, CO: National Park Service, Historic Preservation Division.
- 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.
- Watmough, B.R. 1978. Observations on nocturnal feeding by night herons *Nycticorax nycticorax*. *Ibis* **120**: 356–358.
- Wheelright, N.T., Lawler, J.J. & Weinstein, J.H. 1997. Nest-site selection in Savannah Sparrows: using gulls as scarecrows? *Anim. Behav.* **53**: 197–208.
- White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**(Suppl. 1): S120–S139.
- Wiklund, C.G. 1982. Fieldfare (*Turdus pilaris*) breeding success in relation to colony size, nest position and association with Merlins (*Falco columbarius*). *Behav. Ecol. Sociobiol.* **11**: 165–172.
- Winkler, D.W. 1996. California Gull (*Larus californicus*). In Poole, A. (ed.) *The Birds of North America Online*. Ithaca,

NY: Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/259>.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**: 164–168.

Young, A.D. & Titman, R.D. 1986. Costs and benefits to Red-breasted Mergansers nesting in tern and gull colonies. *Can. J. Zool.* **64**: 2339–2343.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Correlation matrix for variables used in nest survival models for Black-crowned Night-Heron nests on Alcatraz Island 2010–12.

Table S2. Correlation matrix for variables used in nest survival models for Black-crowned Night-Heron nests on Alcatraz Island 2011–12.