

Breeding Ecology and Conservation of Ground-Nesting Waterbirds
in North America and Southeast Asia

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Dedication

I dedicate this dissertation to my parents, Steve and Linda Claassen, for instilling in me a love of adventure, a scientific curiosity, a passion for the natural environment, and for inspiring me to try to make the world a better place. This dissertation is also dedicated to the Cambodian River Terns – may my work bring greater awareness to their plight and spur conservation action to protect this imperiled population.

Abstract

Waterbird populations have declined around the world as a result of anthropogenic impacts from habitat loss and degradation, direct mortality, reproductive failure, and disturbance from humans and non-native and domestic animals. Specialist species are particularly at risk from changing environmental conditions and disturbances compared to generalist species. Plovers, lapwings, terns, and other waterbird species in the Order Charadriiformes nest on the ground, near water, and in exposed areas with little vegetative cover. As a result of their specialized breeding ecology and habitat requirements, nests of these species are therefore highly vulnerable to animal predation, flooding due to rainfall and hydrologic fluctuations, and disturbance from humans and domestic animals. Different social, economic, and political situations among world regions present distinct opportunities and challenges for implementing species conservation. In this study, I explore breeding ecology and conservation of threatened ground-nesting waterbirds in two different systems: 1) Piping Plovers *Charadrius melodus* that breed on lakeshore beaches in the Great Lakes region of the United States, and 2) a community of six species, including River Tern *Sterna aurantia*, River Lapwing *Vanellus duvaucelii*, Great Thick-knee *Esacus recurvirostris*, Indian Thick-knee *Burhinus indicus*, Small Pratincole *Glareola lactea*, and Little Ringed Plover *Charadrius dubius*, that nest on river sand and gravel bars in the Mekong River basin in Cambodia. First, I examine factors affecting nest survival and renesting, and compare *in situ* and *ex situ* management scenarios to evaluate the potential efficacy of egg salvage as a means to augment the Great Lakes Piping Plover population. Second, I investigate factors affecting nest and chick survival of riverine birds in Cambodia, and evaluate the effectiveness of a direct

payment nest protection program to improve reproductive success. Third, I examine factors affecting multi-scale habitat selection, and the consequences of habitat selection on reproductive success of riverine birds in Cambodia. This study provides valuable new information that will aid ongoing conservation efforts for threatened ground-nesting waterbirds such as the Piping Plover in North America and riverine birds in Southeast Asia. This work also has implications for conservation of threatened species more broadly.

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Preface

The three chapters of this dissertation each represents a separate investigation into breeding ecology and conservation of ground-nesting waterbirds in Order Charadriiformes. Chapter 1, “Factors influencing nest survival and renesting by Piping Plovers in the Great Lakes region” was published in the journal *The Condor* in 2014. Chapter 2, “Effectiveness of direct payments to increase reproductive success of sandbar-nesting river birds in Cambodia” was accepted for publication in the journal *Bird Conservation International* in 2016. Chapter 3, “Consequences of multi-scale habitat selection on reproductive success of riverine sandbar-nesting birds in Cambodia” is intended for publication in a yet-to-be-determined peer-reviewed scientific journal. The formatting of chapters 1 and 2 follows the requirements of the specific journals in which they were published or accepted for publication, while Chapter 3 does not follow the format of a specific journal; thus, formatting differs slightly among the three chapters. The singular pronoun “I” is used in the dissertation abstract, acknowledgments, and general introduction, while the plural pronoun “we” is used within the three chapters to acknowledge the contributions of co-authors. Co-authors include Francesca J. Cuthbert (chapters 1-3), Todd W. Arnold (chapters 1-3), James D. Forester (chapter 3), Erin A. Roche (chapter 1), Sarah P. Saunders (chapter 1), and Ko Sok (chapter 2). However, as lead author I am responsible for all content.

Introduction

Globally, 38% of waterbird populations are declining, with 33% decreasing in North America and 51% in Asia (Wetlands International 2012). Moreover, 24% of all waterbird species in the world are classified as globally threatened or near-threatened (Wetlands International 2012). Anthropogenic impacts from increasing human population and economic growth are the primary causes of waterbird population declines worldwide; impacts from anthropogenic sources include habitat loss and degradation, direct mortality, reproductive failure, and disturbance from humans and non-native and domestic animals (Kirby et al. 2008, Sutherland et al. 2012, Wetlands International 2012, Cruz et al. 2013).

Reproductive success is an important measure of avian productivity and is often the focus of conservation efforts for declining species (Sutherland et al., 2004). Recovery of threatened bird species frequently requires management interventions aimed at improving reproductive success rates by mitigating anthropogenic effects, such as preventing egg harvest, protecting critical breeding habitat, minimizing detrimental human activities, and in more extreme cases, to implement *ex situ* conservation measures such as captive breeding (Sutherland et al., 2004). Specialist species are particularly at risk from changing environmental conditions and disturbances compared to generalist species (Clavel et al., 2011). Many waterbirds, such as plovers, lapwings, terns, thick-knees, and pratincoles, nest on the ground, near water, and in exposed areas with little vegetative cover. As a result of their specialized breeding ecology and habitat requirements, nests of these species are therefore highly vulnerable to animal predation,

flooding due to rainfall and hydrologic fluctuations, and disturbance from humans and domestic animals (Sanders and Maloney 2002, Cruz et al. 2013).

Although ground-nesting waterbirds in North America and Southeast Asia experience broadly similar threats from anthropogenic impacts of habitat loss and degradation, predation, and human disturbance, the different social, economic, and political situations in these two regions of the world present distinct opportunities and challenges for implementing species conservation. In North America, conservation efforts for many threatened species have been ongoing for decades with considerable support from federal and state agencies, non-profit organizations, universities, and the public (Parnell et al. 1988, Boere et al. 2006). In contrast, species conservation in Southeast Asia is still in a nascent stage, having only begun recently and implemented with much less governmental and institutional support than more developed regions of the world such as North America (Boere et al. 2006, Sodhi et al. 2010, Clements et al. 2010). Moreover, compared to more developed regions of the world, threatened avian species in poor, developing nations such as in Southeast Asia face greater risks from hunting and harvest of eggs and chicks by local people for food and trade (Sok et al. 2012, Wright et al. 2013).

In this dissertation I explore breeding ecology and conservation of threatened ground-nesting waterbirds in two different systems: 1) Piping Plovers *Charadrius melodus* that breed on lakeshore beaches in the Great Lakes region of the United States, and 2) a community of six species, including River Tern *Sterna aurantia*, River Lapwing *Vanellus duvaucelii*, Great Thick-knee *Esacus recurvirostris*, Indian Thick-knee *Burhinus indicus*, Small Pratincole *Glareola lactea*, and Little Ringed Plover *Charadrius dubius*, that nest

on river sand and gravel bars in the Mekong River basin in Cambodia. In Chapter 1, I examine factors affecting nest survival and renesting, and compare *in situ* and *ex situ* management scenarios to evaluate the potential efficacy of egg salvage as a means to augment the Great Lakes Piping Plover population. In Chapter 2, I investigate factors affecting nest and chick survival of riverine birds in Cambodia, and evaluate the effectiveness of a direct payment nest protection program to improve reproductive success. In Chapter 3, I examine factors affecting multi-scale habitat selection, and the consequences of habitat selection on reproductive success of riverine birds in Cambodia. This dissertation provides valuable new information that will aid ongoing conservation efforts for threatened ground-nesting waterbirds such as the Piping Plover in North America and riverine birds in Southeast Asia. This work also has implications for conservation of threatened species more broadly.

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CHAPTER 1:

Factors Influencing Nest Survival and Renesting by Piping Plovers in the Great Lakes Region

INTRODUCTION

Renesting is an important reproductive strategy, especially among bird species with high rates of nest failure (Sandercock et al. 1999, Hipfner 2001, Arnold et al. 2010, Lishman et al. 2010). However, the relative value of renesting is tempered by the fact that renesting attempts may be less successful or produce poorer quality young than earlier nesting attempts. For many species, clutch size and nest survival decline as the breeding season progresses (Klett and Johnson 1982, Tjørve and Underhill 2008, Verhulst and Nilsson 2008), and replacement nests, which necessarily occur later in the year than initial nests, may have smaller clutches and lower survival rates than first nests (Storaas et al. 2000, Suarez et al. 2000, Gregg et al. 2006, Devries et al. 2008). Likewise, pre- and post-fledging survival may be lower for young hatched later in the season (Roche et al. 2008, Gruebler and Naef-Daenzer 2010, Brudney et al. 2013), and for young hatched from renesting attempts (Martin and Hannon 1987, De Neve et al. 2004, Becker and Zhang 2010). Potential reasons for seasonal declines in reproductive success include decreases

in food availability (Verhulst & Nilsson 2008), changes in predator dynamics or environmental conditions (Grant et al. 2005), variation in parental quality (Saunders et al. 2012), or time constraints on migration or other post-breeding activities (Verboven and Visser 1998). Also, lower survival of replacement nests may occur if physical condition of breeding adults declines with subsequent nesting attempts (Wendeln et al. 2000, Gasparini et al. 2006).

Even among species that are capable of renesting, not all individuals will renest after nest failure. Renesting propensity, the likelihood of renesting following nest failure, may vary according to timing of the breeding season (Amat et al. 1999, Brinkhoff et al. 2002), number of previous nesting attempts (Arnold et al. 2010), age of the previous nest at the time of nest failure (Fondell et al. 2006, Antzak et al. 2009), or the age, experience, and physical condition of breeding adults (Wendeln et al. 2000, Arnold et al. 2010).

Timing of a renesting attempt is influenced by date of previous nest failure and the amount of time it takes for a bird to initiate a replacement nest (i.e., the renesting interval). The renesting interval may vary according to season (Wendeln et al. 2000, Becker and Zhang 2010), number of previous nesting attempts (Arnold et al. 2010), age of the previous nest (Fondell et al. 2006), or quality of breeding adults (Wendeln et al. 2000). Also, renesting intervals may vary depending on type of nest failure (e.g., predation vs. abandonment) or whether breeding birds change mates or locations between subsequent nesting attempts (Haig and Oring 1988, Amat et al. 1999, Lishman et al. 2010).

The Piping Plover (*Charadrius melodus*) is a small migratory shorebird with breeding populations in the Atlantic Coast, Great Plains, and Great Lakes region, the

latter of which is federally endangered (COSEWIC 2003, USFWS 2003). Great Lakes Piping Plover numbers declined dramatically from the 1950s to 1990, prompting intensive conservation efforts (USFWS 2003). Low reproductive success is thought to have contributed to the species' decline, and in the U.S., conservation efforts have focused primarily on protecting Piping Plover breeding sites in the Great Lakes region, including the use of predator exclosures to safeguard nests and beach closures to minimize human disturbance (USFWS 2003). Because Piping Plovers nest on the ground, near water, and in exposed areas with little vegetative cover, their nests are especially vulnerable to predation, flooding, and disturbance (Haig and Oring 1988, Wemmer et al. 2001, Knetter et al. 2002, USFWS 2003). Piping Plovers are known to renest following the loss of earlier nests, and may renest several times during the breeding season if their nests continue to fail (Cairns 1982, Haig and Oring 1988). A study of individually marked Piping Plovers in Manitoba found no difference in hatching success between first nests and renests (Haig and Oring 1988), but causes and consequences of individual variation in renesting propensity were not investigated. In a study of unmarked Piping Plovers in Saskatchewan, seasonal declines in hatching success and clutch size were speculated to be an effect of renesting (Harris et al. 2005); however, first nests could not confidently be separated from renests. The Great Lakes population has a high proportion (>90%) of individually color-banded adults, presenting an opportunity to investigate sources of variation in renesting behavior by individual Piping Plovers.

From a conservation perspective, it is important to assess how renesting contributes to overall reproductive success of Great Lakes Piping Plovers and to ensure the effectiveness of management strategies employed to augment this federally

endangered population. One current strategy is egg salvage from recently abandoned nests for captive rearing and release of fledged chicks back into the wild (Powell and Cuthbert 1993, Powell et al. 1997, Roche et al. 2008). Proactive population augmentation has also been considered (USFWS 2003), which would entail active collection of eggs from first nests for captive rearing, under the assumption that wild birds will renest with little impact to overall reproductive success. However, captive-reared individuals have lower survival and reproductive success than wild-reared birds (Roche et al. 2008). Furthermore, not all wild individuals will renest following clutch removal, and replacement clutches will be initiated later in the season and likely have lower reproductive success. Thus, any serious consideration of proactive clutch removal for captive rearing must properly measure the costs associated with renesting.

The objectives of our study were to investigate causes and consequences of variation in: 1) timing of nest initiation, 2) clutch size, 3) daily nest survival, 4) renesting propensity, and 5) length of the renesting interval. Specifically, we sought to understand and quantify the contribution that renesting behavior makes to overall reproductive success, while also measuring the cost of delay which is an inevitable consequence of renesting. This information has important management implications for Great Lakes Piping Plovers and other shorebird populations whose nests are affected by incidental take (McGowan and Ryan 2009). Our results can also be used to assess the costs and benefits of proactive versus salvage egg collection programs for Great Lakes Piping Plovers.

METHODS

Study Area

Since 1993, Piping Plovers have been banded with USGS metal and Darvic colored bands and monitored annually in the Great Lakes region of North America. The study area included public and private sites on lakes Michigan, Huron, and Superior that were used by breeding Piping Plovers during 1993 – 2010; the majority of sites were in Michigan and a few were in eastern Wisconsin and southern Ontario, Canada (figure 1 in Brudney et al. 2013). Sites consisted of wide, sparsely vegetated sand and gravel lakeshore beaches, which are the preferred breeding habitat of Piping Plovers (Wemmer et al. 2001, USFWS 2003).

Data Collection

We analyzed Piping Plover nest data that were collected from 1993 – 2010 by a network of contributing partners as part of an ongoing recovery effort for the Great Lakes population (USFWS 2003). Shoreline surveys were conducted each year from late April to early August to locate nesting sites of Piping Plovers. Once located, nests were monitored until termination (i.e., until all eggs either hatched or were determined to have failed). Nests were usually visited every 1 – 2 days, although a few sites (~7%) were visited less regularly with intervals between visits ranging from 3 – 9 days. For each nest, data were collected on clutch size, nesting attempt, nest fate (success or failure), date of hatch or failure, cause of nest failure, and adult identities. In cases of nest abandonment (i.e., nest unattended for $\geq 4 - 5$ hours), eggs were collected for captive rearing. Predator exclosures consisting of wire fencing and plastic mesh were erected immediately upon location of a nest (USFWS 2003). Small, wire mesh box exclosures were used during egg laying, and until full-sized exclosures could be erected (Melvin et al. 1992, USFWS

2003). Predator exclosures were used for nearly all nests; 100% of nests have been protected by this method since 2004 (Saunders et al. 2012). Additionally, rope fencing and signs were used to cordon off many of the nesting beaches to reduce human disturbance. Adult Piping Plovers were nest-trapped during mid-incubation and fitted with unique individual colored band combinations (USFWS 2003).

We investigated causes of variation in nest initiation date, clutch size, daily nest survival rate (DSR), renesting propensity, and length of the renesting interval. We examined only the nesting period (egg laying and incubation stages) up until hatching. For nest survival analyses, a nest was defined as successful if at least one egg hatched under natural conditions, or if the nest was brought to full term (34 days) before eggs were salvaged for captive rearing. For renesting propensity analyses, a nest was considered to have failed if eggs only hatched in captivity, and was only considered successful if at least one egg hatched under natural conditions. We defined renesting propensity as the proportion of individuals that renested following a failed previous nesting attempt (Arnold et al. 1993, Fondell et al. 2006). We calculated the renest interval as the number of days between failure of a previous nest and initiation of the replacement nest; for example, if a nest failed on 3 June and the first replacement egg was laid on 10 June, then the renest interval was estimated as 7 days. Number of nesting attempts was tallied assuming that we found all initiated nests, but it is likely that we missed some nests that were destroyed during early laying (McPherson et al. 2003), so counts of previous nests represent minimum values. Nest initiation dates were estimated by backdating, assuming a 2-day laying interval between eggs (Elliott-Smith and Haig 2004, E. A. Roche personal observation) plus a 28-day incubation period after the last egg was

laid (see Results section). For nests that were found after the last egg was laid, but failed prior to hatching and thus had unknown initiation dates (6% of nests), we assumed the nests were the average age of discovery (7 days old), and backdated accordingly. Birds of unknown age were assigned a minimum age of 1 the first time they were captured (Roche et al. 2010, Saunders et al. 2012). We considered a nest to be abandoned if adults were observed again during the breeding season or in a subsequent year, and we considered an adult to have died if it disappeared early in the breeding season during incubation and was not seen again during that breeding season or any subsequent years (Neuman et al. 2004, Roche et al. 2010).

For renesting analyses, we excluded birds presumed to have died (Neuman et al. 2004, Roche et al. 2010) and therefore incapable of renesting, but the surviving mate was included in the analyses. For renesting propensity analyses, we only included breeding attempts that failed during the nesting stage; we excluded eight pairs that renested after complete or partial brood mortality, and we also excluded one female that renested after successfully fledging a first brood. For clutch size analyses, we excluded all nests that failed prior to clutch completion, and one-egg clutches that had likely experienced partial predation before they were discovered. Nesting attempts were divided into three categories: first attempts, second attempts, and \geq third attempts. Because birds did not always reunite with their former mate for renesting, we analyzed male and female renesting attempts separately for renesting propensity and renesting interval analyses. We assumed that a renesting attempt was a continuation nest (i.e., replacement nests of birds that lost a nest during egg laying and renested soon after, with no interruption in laying) if nest loss occurred during egg laying and the replacement nest was initiated within five

days of nest loss. In the nest survival analyses, inviable nests that were continuously tended by adults were treated as successful on the 34th day after they were initiated (i.e., average laying and incubation periods for a four-egg clutch), at which point they were censored from further analysis. However, inviable nests were treated as failures for purposes of investigating renesting propensity.

Statistical Analyses

Nest survival analyses were conducted using the NLMIXED procedure with SAS software (Rotella et al. 2004, SAS Institute, Cary, NC), which provides maximum likelihood estimates of daily survival rates (DSR) and allows for interval censoring, daily covariate values, and a single random effect. We used a logit link function to constrain DSR to be between zero and one. Because penultimate visits to nests were not routinely recorded during nest monitoring efforts, we estimated dates of penultimate visits based on the nest monitoring frequency for each site. For ease of interpretation, we converted estimates of DSR into cumulative nest survival (the probability of a nest surviving the entire nesting period) by taking the product of predicted DSR for each day of an average 34-day exposure period, using appropriate covariate values for each day (Shaffer and Thompson 2007); most importantly, this involved incrementing nest age by one day for each successive day.

We investigated sources of variation in renesting propensity, renesting interval, clutch size, and nest initiation date using general linear models (glm function) and generalized linear mixed models (package lme4; Bates and Sarkar 2006) using R statistical software (version 2.15.1; R Development Core Team 2012). For renesting propensity analyses, we used the binomial family (logit link). For nest initiation date,

renesting interval, and clutch size analyses, we compared models using Gaussian and Poisson distributions, and determined that Gaussian models fit better.

For each of the five response variables (DSR, nest initiation date, clutch size, renesting propensity, and renesting interval), we investigated variation in response to relevant covariates such as: date of nest initiation, date of nest failure, nest age, nesting attempt, year, cause of nest failure, male age, female age, sex of adult, clutch size, whether an adult changed location between consecutive nesting attempts, and whether an adult changed mates between consecutive nesting attempts. For each analysis we only included covariates for which we had formulated *a priori* hypotheses regarding how each covariate might explain variation in the specific breeding parameter of interest (Table 1). For date, we considered day 1 = 20 April. We considered nest age = 1 to be the day the first egg was laid, then incremented daily. We treated cause of nest failure as a categorical factor with five levels: predation, flooding, abandonment, adult mortality, or all eggs inviable.

To avoid overfitting models and because some covariates were correlated (e.g., nest initiation date and nesting attempt), we used a forward selection approach to model building, starting with the simplest model containing an intercept-only term and sequentially adding variables to each model. At each stage of the model selection process, we moved forward with the best-supported model. We evaluated models using an information-theoretic approach, ranking models according to their Akaike's Information Criteria values adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). If a model under consideration included a main effect (linear term) for a covariate, we also considered the quadratic term for that covariate. We identified the

best-supported model in each candidate set based on minimal AIC_c and the largest Akaike weight (w_i), which is the probability that each model is best, conditional on the data and model set (Burnham and Anderson 2002). We considered a model to be competitive if it was ≤ 2 AIC_c units of the best model, as long as it was not merely the best model plus one uninformative parameter (Burnham and Anderson 2002, Arnold 2010).

Because we assumed there was variation between years, and we wanted to account for this source of heterogeneity, we included year as an *a priori* random effect. Thus, for each response variable, our base model contained an intercept term and a random year effect. However, if random year effects were not supported ($\sigma^2_{\text{year}} = 0$; Zuur et al. 2009) in the best model from the resulting candidate set, we removed random year effects and repeated the entire model-selection procedure using fixed effects only. Unless otherwise indicated, means are reported ± 1 standard deviation (SD).

Removal versus Non-removal of Clutches

We compared Piping Plover productivity (number of one-year-old recruits into the Great Lakes population) under two different management scenarios: 1) removal of eggs from first nests for captive rearing, and 2) leaving eggs *in situ*. We assumed a sample size of 20 nesting pairs under each scenario. Under the captive rearing scenario, we assumed eggs were removed at nest age = 10; we considered clutch removal to be nest loss. Total productivity (number of one-year-old recruits from first nests and renests) was compared between the captive rearing and *in situ* management scenarios. We estimated productivity of first nests as: productivity = sample size of clutches * clutch size (this study) * nest success (hatching success of captive-incubated eggs, Roche et al. 2008, or cumulative

nest survival of wild clutches, this study) * fledging success (captive-reared fledging success, Roche et al. 2008, or wild fledging success, Brudney et al. 2013) * hatch year (HY) survival (Saunders et al. 2014) * reproductive value of one-year old recruits (0.75 for captive-reared, or 1 for wild one-year-old recruits, Roche et al. 2008). We estimated productivity of renests as: productivity = sample size of nesting pairs that lost first nests * renesting propensity (this study) * clutch size of renests (this study) * nest success of renests (this study) * fledging success from renests (Cuthbert and Roche 2010) * HY survival (Saunders et al. 2014). Estimates of renesting propensity, renest interval (and hence initiation date for replacement nests), clutch size, and renest survival were made using best-supported models from this study, based on predicted timing of renests.

RESULTS

We obtained data from 772 nests over 18 years (1993 – 2010). The average age of nests at discovery was 7.0 ± 6.7 days old. For 328 nests that were monitored from egg laying until hatching, the mean exposure period was 33.7 ± 2.3 days from the day the first egg was laid, and 27.7 ± 2.3 days from the day the last egg was laid.

Nest Initiation Date

The mean initiation date for first nests was 17 May \pm 13 days (90% range: 30 April – 10 June, $n = 674$). The best-supported model of nest initiation date included a random effect of year and quadratic effects of both female and male age (Tables 2 and 3). Older adults initiated nests earlier in the season than did younger adults, with the greatest advancements occurring between ages 1 and 3 (Figure 1). The effect of age was stronger for females than males; a nine-year-old female nested ~14 days earlier than a one-year-

old female, but a nine-year-old male only nested ~9 days earlier than a one-year-old male (Figure 1).

Clutch Size

Observed size of completed clutches was 3.9 ± 0.4 eggs (range: 2 – 6 eggs; $n = 739$), excluding four one-egg nests that likely experienced partial predation. The best-supported model of clutch size included a quadratic effect of nest initiation date (Tables 2 and 3); this model received nearly all of the support among models in the candidate set (Table 2). Clutch size increased slightly from 3.8 ± 0.04 (SE) for nests initiated early (20 April) to 3.9 ± 0.02 (SE) for nests initiated mid-season (25 May), but then declined to 3.4 ± 0.07 (SE) for nests initiated late in the season (25 June; Table 3).

For female plovers that lost nests during laying, 21 of 75 renesters (28%) produced continuation nests. On average, continuous layers produced 6.4 ± 1.4 consecutive eggs (range: 4 – 8 eggs); only 9% of continuous layers stopped laying after 4 consecutive eggs. Because the occurrence of supranormal continuation clutches may have influenced model results regarding effects of female nesting attempt on variation in clutch size, we conducted a *post hoc* analysis with continuation nests removed from the dataset, but results were unchanged.

Nest Survival

Our sample included 772 nests (680 first nesting attempts and 92 nests that were second or later nesting attempts for at least one parent). Apparent nest success was 76% (recall that nearly all nests were protected by predator exclosures). Initiation date had the most influence on DSR, and all top models included the quadratic term of this covariate. The best-supported model of DSR also included a quadratic effect of nest age, and a linear

effect of male age (Table 2). Parameter estimates from the best-supported model showed that DSR increased with nest age from nest initiation until late in incubation, but declined as nests approached hatching age (Table 3, Figure 2). DSR increased with nest initiation date until mid-season (~20 May), but then declined among late season nests (Figure 3; DSR was converted to cumulative nest survival for ease of interpretation). Also, DSR increased with age of the male parent (Table 3). Cumulative nest survival averaged 0.70 ± 0.04 (SE) for a one-year-old male, 0.74 ± 0.02 (SE) for a four-year-old male (mean age), and 0.81 ± 0.05 (SE) for a ten-year-old male for nests initiated on 15 May.

Renesting Propensity

Piping Plovers replaced 138 of 280 failed nests, for a 49% apparent renesting propensity; there was no difference in apparent renesting propensity between males and females. The greatest number of nesting attempts in a single season was five; the same pair renested four times, with a total of 15 eggs laid. Estimates of renesting propensity represent minimum values because some nests likely failed prior to detection.

Nest losses were due to predation (34%), flooding (25%), death of a breeding adult (20%; surviving adult was included in the analysis), abandonment (17%; both adults still alive), and clutch inviability (4%). In 12 cases of inviable clutches, eggs were removed 7 – 16 days after the predicted hatching date, but none of these birds renested; however, models that included inviable nests as a separate cause of nest failure did not converge, so we removed inviable nests from the dataset and reanalyzed data for the remaining 268 nest failures with four rather than five causes of nest failure.

Renesting propensity was most strongly affected by date; the inclusion of date covariates resulted in models with the lowest AIC_c values. Nest failure date explained

variation in renesting propensity better than nest initiation date, so was retained in subsequent models. The best-supported model of renesting propensity included a random effect of year, a quadratic effect of nest failure date, cause of nest failure, and nesting attempt (Table 2). Parameter estimates from the best-supported model showed that renesting propensity decreased according to the date of nest failure (Table 3, Figure 4A, 4B). Renesting propensity was also related to cause of failure, with flooding losses being most likely to be replaced, followed by predation, abandonment, and death of a mate (Figure 4A). Additionally, renesting propensity increased for birds with a greater number of prior nesting attempts (Figure 4B).

Renesting Interval

The mean observed renesting interval was 5.9 ± 4.5 days ($n = 138$). The best-supported model of renesting interval included a random effect of year, a quadratic effect of nest age, and an effect of changing mates. This model received nearly all of the support among models in the candidate set (Table 2). Estimated renesting intervals were ~4 days when nest failure occurred shortly after initiation, but increased to ~8 days when nest failure occurred during mid-incubation. Also, renesting intervals were ~3 days longer for birds that renested with a new mate than for individuals that renested with the same mate; 80% of mate changes ($n = 25$) were due to death of a previous mate.

Removal versus Non-removal of Clutches

We compared potential productivity (number of one-year-olds recruited into the population) between two management scenarios: 1) removal of initial clutches for captive rearing, and 2) leaving clutches *in situ*. Under the captive rearing scenario, removal of 20 first nests at age 10 days resulted in the equivalent of 3.7 one-year-old recruits from

captive-reared first nests and 4.0 one-year-old recruits from wild renests of those 20 pairs, for a total of 7.6 one-year-old recruits (Table 4). Under the non-removal scenario, leaving all 20 first nests *in situ* resulted in 12.3 one-year-old recruits from first nests, and 1.0 one-year-old recruits from natural renests, for a total of 13.3 one-year-old recruits. Thus, clutch removal resulted in 5.7 fewer one-year-old recruits into the population, and only 57% productivity compared to leaving clutches *in situ*.

DISCUSSION

Renesting is an important component of Piping Plover reproduction, as nearly half of all individuals renested after failure of an earlier nest. In a natural scenario, where nests would not be protected by individual predator exclosures, renesting would undoubtedly play an even more important role. However, we found that renests were less productive than initial nests, not because renests are less productive per se, but because they were initiated later in the season and consequently had lower average clutch size and nest survival (Table 2, Figure 3), as well as lower chick survival (Brudney et al. 2013) and post-fledging survival (Saunders et al. 2014). Other studies of Piping Plovers have also found strong seasonal effects on reproductive success (Harris 2005, Saunders et al. 2012, Brudney et al. 2013), and any factors that cause plovers to nest later, including renesting, are likely to lead to lower breeding productivity. Studies of other precocial species have found that after controlling for later nest initiation date, renests were as productive as initial nests (Amat et al. 1999, Arnold et al. 2010). In this study, nest survival was influenced by nest initiation date, but not later nesting attempt (Table 2), suggesting that Piping Plover reproductive success is better explained by seasonal effects, rather than

prior investments in clutch formation and incubation. We speculate that seasonal declines in reproductive success may have been a result of diminishing food resources for adults or chicks, changes in predator abundance or behavior, or increased frequency or intensity of late summer storm surges. Alternatively, seasonally declining reproductive success may have indicated lower parental investment in late season nests given reduced survival rates for late-hatched chicks and fledglings (Roche et al. 2008, Brudney et al. 2013).

Nesting attempt was an important factor in explaining renesting propensity of adults, although less so than seasonal effects related to date of failure of the previous nesting attempt (Tables 2 and 3). Even though renesting propensity declined to zero towards the end of the breeding season, renesting propensity was higher for individuals that had a greater number of previous nesting attempts than for individuals with fewer previous nesting attempts (after controlling for nest failure date; Figure 4B). This result was contrary to our *a priori* hypothesis that renesting propensity would decline with later nesting attempt due to costs of reproduction. Instead it suggests that individual quality is an important determinant of renesting propensity; proven renesters are more likely to renest repeatedly, owing to some unmeasured aspect of individual quality.

We used age of breeding adults as an indication of adult breeding quality. A number of studies of other species have found that older birds nest earlier (Wendeln et al. 2000, Becker and Zhang 2010), have higher nest survival rates (Devries et al. 2008), and have a greater likelihood of renesting after nest loss (Wendeln et al. 2000, Fondell et al. 2006, Arnold et al. 2010). In our study, nest survival increased with age of the breeding male (Tables 2 and 3). Renesting propensity was not affected by male or female age. However, both nest survival and renesting propensity were strongly influenced by

initiation date, and older males and females initiated nests earlier than younger individuals (Figure 1). Saunders et al. (2012) had similar results with respect to the influence of adult age on hatching date.

We found that nest survival was more strongly influenced by male than female age (Table 2). Male Piping Plovers arrive on the breeding grounds before females, and older birds generally arrive before younger individuals (Stucker et al. 2010). Males also have the primary role in territory establishment and defense (Cairns 1982), and exhibit higher breeding site fidelity than females (Haig and Oring 1988). Higher nest survival of older males in this study may have been due to earlier arrival times, and greater ability to establish and maintain high-quality breeding territories. Roche et al. (2010) found that breeding females had higher mortality rates than males, and older females had higher mortality rates than younger females. In this study, perhaps the benefits of female age and experience on nest survival were counteracted by a higher probability of death for older females. Interestingly, Saunders et al. (2012) found that fledging success was more strongly influenced by age and experience of females than males. Females generally depart breeding grounds before males (Cairns 1982), and because older females nested earlier, they may have been less likely to abandon their broods before they fledged.

Daily nest survival increased from nest initiation until mid-incubation, but then followed a quadratic pattern of decline among older nests (Figure 3). The apparent decline in survival of older nests may be an artifact of fitting a quadratic model to data exhibiting a strong pattern during early nesting; however, other investigators have found similar patterns among waterfowl, and speculated that lower survival of older nests may be related to changes in adult behavior close to hatching (Grand et al. 2006, Grant and

Shaffer 2012). Circumstantial evidence suggests that adult Piping Plovers also change their behavior, becoming increasingly attentive and restless close to hatching (S.P. Saunders, personal observation). We initially considered whether increased activity by attendant parents and/or increased noise associated with hatching might have increased the probability of nest loss to predators near hatching. However, during the last week of incubation prior to hatching, the proportion of clutch loss from predation decreased from 39% (average during first four weeks of the nesting period) to 26%, but death of a breeding adult increased from 18% (average during first four weeks of the nesting period) to 30%. We speculate that increased activity close to hatching may have increased the probability of predation on attending adults, thus indirectly causing nest failure.

Although age of the previous nest at the time of nest failure did not influence renesting propensity, it did influence length of the renesting interval (Table 2). Renesting intervals increased with age of the previous nest at the time of failure, and were shortest for nests that failed during egg laying. Adults with nests that failed early in the incubation period had invested less time and energy in the previous nest, and females that lost clutches during egg laying potentially still had enlarged oviducts and developing follicles allowing prompt initiation of a continuation nest.

Renesting intervals were also ~3 days longer for adults that needed to find a new mate (Table 2). Divorce (i.e. intra-year mate switching when both members of a pair were alive; Choudhury 1995) among Piping Plovers was rare, and 80% of intra-year mate changes were the result of the death of a previous mate.

After controlling for date of failure and nesting attempt, death of a mate resulted in the second lowest renesting propensity after egg inviability (Figure 4A). Birds did not

renest if their clutches were inviable, even in cases where it was still early enough in the season for them to potentially do so. However, with the exception of one infertile male (inviable clutches in several different years) and one female who only survived a single breeding season, all birds with inviable clutches nested successfully in subsequent years. Renesting propensity was highest among birds with nests that failed due to flooding or clutch predation (Figure 4A). As with other shorebirds (Sandercock et al. 1999, Lishman et al. 2010), renesting by Piping Plovers is likely an evolutionary adaptation to compensate for high rates of egg loss to predators and weather-related events, rather than other causes of nest failure such as clutch inviability or mate loss. We speculate that the failure to renest following death of a mate may be due to constraints imposed by lack of available mates late in the season, or may reflect individual restraint when faced with longer renesting intervals and subsequent seasonal limitations resulting from delayed renesting.

Nearly all nests were protected by predator exclosures, which likely affected renesting propensity. Renesting rates in this study may have been lower than they would have been naturally because nests likely survived longer before failing, and thus timing of nest losses occurred later in the season and after greater energy investments by incubating adults. Also, other studies have shown that use of exclosures may increase mortality risks for adult plovers (Johnson and Oring 2002, Murphy et al. 2003, Neuman et al. 2004). In this study, the likelihood of renesting was lower following death of a mate than for other types of nest loss (Figure 4A). Although there was no direct evidence of mortality due to exclosure use in this study, if exclosures contributed to adult disappearances, they may have thus indirectly affected renesting propensity of the surviving adult.

Clutch size exhibited a quadratic pattern of decline; model-estimated clutch size increased from 3.8 to 3.9 from early to mid-season, before declining to 3.4 at the end of the breeding season (Tables 2 and 3). The slightly lower clutch size earlier in the season, compared to mid-season may have been a result of low spring temperatures, a variable reported to affect clutch size in a closely related shorebird species (Nol et al. 1997). In general, clutch size of Great Lakes Piping Plovers declined with later nest initiation date, which is consistent with findings from studies of Piping Plovers elsewhere (Cairns 1982, Harris et al. 2005). Although Piping Plovers have a modal clutch size of 4 eggs, we found that the frequency of 2- and 3-egg clutches increased towards the end of the breeding season. Continuation nesters were able to lay 5 – 8 eggs in normal succession, and the greatest number of eggs laid by a female in a single season was 15, suggesting that egg production capability of females was likely not the limiting factor for clutch size toward the end of the breeding season.

Although our results indicate that nest survival and renesting by Great Lakes Piping Plovers are strongly influenced by seasonal variation, parental quality was somewhat important as well. Older males had higher nest survival (Tables 2 and 3), and older males and females initiated nests earlier in the breeding season (Figure 1). Interestingly, a few Piping Plovers were able to produce replacement nests throughout the breeding season if their nests continued to fail; five nesting attempts was the maximum number recorded for a single bird in a single season. Although we did not find an effect of parent age per se on renesting propensity, perhaps other indicators of individual quality, such as foraging efficiency (Lescroël et al. 2010) or establishment of high-quality

territories as a result of early arrival or competitive ability (Marra 2000), may better explain variation in renesting propensity among individuals.

Implications for Conservation

We compared two potential management strategies for Great Lakes Piping Plovers: 1) removing initial clutches for captive rearing, and 2) leaving clutches *in situ*. Our results suggest that removal of clutches for captive rearing led to fewer one-year-old Piping Plovers recruited into the Great Lakes population than leaving clutches *in situ* (Table 4). Lower productivity under the clutch removal scenario was primarily a result of reduced survival of captive-reared chicks compared to wild chicks (Roche et al. 2008), and renesting could only partially compensate for the removal of earlier nests.

Overall, about half the Piping Plovers in the Great Lakes renested after failure of an earlier nest. However, renesting propensity varied according to date and cause of previous nest failure; renesting was more likely to occur following early-season predation rather than a late-season weather event (Figure 4A). Replacement nests are necessarily initiated later in the season and thus produce smaller clutches (Tables 2 and 3), and have lower chances of nest survival (Figure 3) and fledgling survival (Brudney et al. 2013). Based on our results, proactive removal of first nests for captive rearing is not recommended for this endangered population, although egg collection may be warranted in cases of probable nest failure (e.g., nest located within a flood zone). Our results suggest that as the breeding season progresses, conservation managers should be increasingly proactive with *in situ* nest protection efforts (e.g., enhanced predator control efforts), rather than relying on collection of eggs for captive rearing.

Table 1. *A priori* hypotheses about variables affecting daily nest survival rate (DSR), nest initiation date, renesting propensity, renesting interval, and clutch size of Great Lakes Piping Plovers during 1993-2010.

Explanatory variable	Abbreviation	A priori hypotheses
Nest initiation date	INITDATE	Later nests will have lower DSR and smaller clutches.
Nest failure date	FAILDATE	Later nest failure date will result in lower adult renesting propensity and longer renesting intervals.
Nesting attempt	ATTEMPT	Later nesting attempts will have lower DSR, lower renesting propensity, longer renesting intervals, and smaller clutches.
Nest age	NESTAGE	Older nests will have higher DSR, lower renesting propensity, and longer renesting intervals.
Cause of nest failure	CAUSE	Renesting propensity will be lower, and renest intervals will be longer, for birds that need to find a new mate if their previous mate died (or was infertile).
Age of adult	M_AGE, F_AGE	Older males (M_AGE) and females (F_AGE) will have higher DSR, earlier nesting, higher renesting propensity, shorter renesting intervals, and larger clutches.
Sex of parent	SEX	Females may have lower renesting propensities and longer renesting intervals due to greater investment in clutch production.

Clutch size	CLUTCH	Because small clutches are likely indicative of poorer quality adults, small clutches will be less likely to be replaced and will have longer renesting intervals.
Location change	LOCATION	Changing location between consecutive nesting attempts will increase the renesting interval.
Mate change	MATE	Changing mates between consecutive nesting attempts will increase the renesting interval.

Table 2. Model selection results of the top 5 models of nest initiation date, clutch size, nest survival, renesting propensity, and renesting interval of Piping Plovers in the Great Lakes region during 1993-2010. Intercept models are also listed for reference.

Model ^a	ΔAIC_c^b	w_i^c	K^d	Dev ^e
Nest Initiation Date^f				
AGE_F ² + AGE_M ²	0	0.573	6	5117.8
AGE_F ² + AGE_M	0.6	0.427	5	5128.1
AGE_F ²	13.9	0.001	4	5151
AGE_F	41.5	0	3	5188.2
AGE_M ²	75.1	0	4	5211.8
Intercept	170.4	0	2	5326.3
Clutch Size				
INITDATE ²	0	0.9997	3	520.4
INITDATE	16.2	0.0003	2	539.3
ATTEMPT_F	36.3	0	2	559.3
ATTEMPT_M	42.4	0	2	565.3
Intercept	45.1	0	1	570.9
Daily Nest Survival (DSR)				
INITDATE ² + NESTAGE ² + AGE_M	0	0.519	6	1846.7
INITDATE ² + NESTAGE ²	0.1	0.47	5	1848.8
INITDATE ² + NESTAGE	3.9	0.011	4	1854.7
INITDATE ² + AGE_M	7.7	0.0002	4	1858.5
INITDATE ²	10.0	0	3	1862.8

Intercept	19.7	0	1	1876.5
Renesting Propensity ^f				
FAILDATE ² + CAUSE + ATTEMPT	0	0.847	8	237.5
FAILDATE ² + CAUSE + NESTAGE	4.8	0.077	8	242.2
FAILDATE ² + CAUSE	4.9	0.073	7	245.3
FAILDATE ² + ATTEMPT	12.8	0.001	5	259.1
FAILDATE ² + NESTAGE	14	0.0008	5	260.2
Intercept	105	0	2	359.4
Renesting Interval ^f				
NESTAGE ² + MATE	0	0.831	5	652.8
NESTAGE ²	3.2	0.169	4	663.3
CLUTCH	19.9	0	3	687
MATE	22.4	0	3	689.4
NESTAGE	29.9	0	3	696.6
Intercept	38	0	2	712.3

^a A superscript² indicates a quadratic effect plus lower order term. + indicates an additive effect. Lowest Akaike's Information Criterion values adjusted for small sample sizes (AIC_c) were: 5185.68 (Nest Initiation Date), 805.94 (Clutch Size), 1876.80 (DSR), 262.54 (Renesting Propensity), and 852.75 (Renesting Interval).

^b The difference in AIC_c value between the model and the best-supported model.

^c Akaike weight.

^d Number of model parameters.

^e Model deviance.

^f All models (including intercept models) contain year as a random effect.

Table 3. Parameter estimates, standard errors, and 95% confidence intervals from the best-supported models of nest initiation date, clutch size, nest survival, nest initiation date, renesting propensity, and renesting interval of Piping Plovers in the Great Lakes region during 1993-2010.

Parameter ^a	Estimate	SE	95% Confidence Interval	
			Lower	Upper
Nest Initiation Date				
INTERCEPT	38.891	1.346	36.254	41.529
AGE_F	-4.778	0.606	-5.966	-3.591
AGE_F ²	0.304	0.06	0.1859	0.423
AGE_M	-3.011	0.638	-4.262	-1.76
AGE_M ²	0.213	0.065	0.085	0.341
Clutch Size				
INTERCEPT	3.886	0.044	3.799	3.973
INITDATE	0.009	0.003	0.002	0.015
INITDATE ²	-0.0002	-0.00005	-0.0001	-0.0003
Daily Nest Survival (DSR)				
INTERCEPT	3.142	0.551	2.061	4.22
INITDATE	0.033	0.022	-0.01	0.076
INITDATE ²	-0.0005	0.0002	-0.0009	-0.0001
NESTAGE	0.101	0.033	0.037	0.165
NESTAGE ²	-0.002	0.0008	-0.0037	-0.0004
AGE_M	0.06	0.043	-0.023	0.143
Renesting Propensity				
INTERCEPT	0.746	1.597	-2.385	3.877
FAILDATE	0.044	0.068	-0.089	0.178
FAILDATE ²	-0.0017	0.0008	-0.0032	-0.0002
CAUSE2 (mate loss)	-1.482	0.454	-2.372	-0.592
CAUSE3 (abandonment)	-0.378	0.497	-1.352	0.596
CAUSE4 (flooding)	0.672	0.458	-0.226	1.571
ATTEMPT	1.139	0.422	0.311	1.966
Renesting Interval				
INTERCEPT	-0.678	0.993	-2.625	1.269

NESTAGE	0.776	0.136	0.509	1.043
NESTAGE ²	-0.018	0.004	-0.026	-0.011
MATE	3.27	0.812	1.679	4.861

^a A superscript² denotes a quadratic term. CAUSE was a categorical factor with four levels: CAUSE1 (predation), CAUSE2 (mate loss), CAUSE3 (abandonment), and CAUSE4 (flooding).

Table 4. Comparison of removing first nests for captive rearing versus leaving first nests *in situ*, in terms of number of one-year-old recruits into the Great Lakes Piping Plover population.

	Captive Component	Wild Component
First nests		
Number of clutches ^a	20	20
Clutch size ^b	4	4
Nest success	0.85 ^c	0.74 ^b
Fledging success	0.90 ^c	0.56 ^d
HY survival ^e	0.08 ^c	0.37 ^e
Reproductive value of 1-year-old recruits ^c	0.75	1
Number of 1-year-old recruits (first nests) ^f	3.67	12.27
Renests		
Number of pairs that lost first nests	20	5.2 ^b
Renesting propensity ^b	0.76	0.76
Clutch size ^b	3.81	3.81
Nest success ^b	0.65	0.65
Fledging success ^g	0.5	0.5
HY survival ^e	0.21	0.21
Number of 1-year-old recruits (renests) ^f	3.95	1.03
Total number of 1-year-old recruits ^h	7.62	13.29

^a Captive component: 20 clutches removed for captive rearing (nest age = 10); wild component: 20 nests left *in situ*.

^b Based on estimates from best-supported model of clutch size, nest survival, or renesting propensity.

^c Rearing success of captive chicks; Roche et al., 2008.

^d Brudney et al., 2013.

^e Saunders et al. 2014.

^f Product of above values.

^g Cuthbert and Roche, 2010, unpublished report.

^h Total number of one-year-old recruits from first nests plus renests.

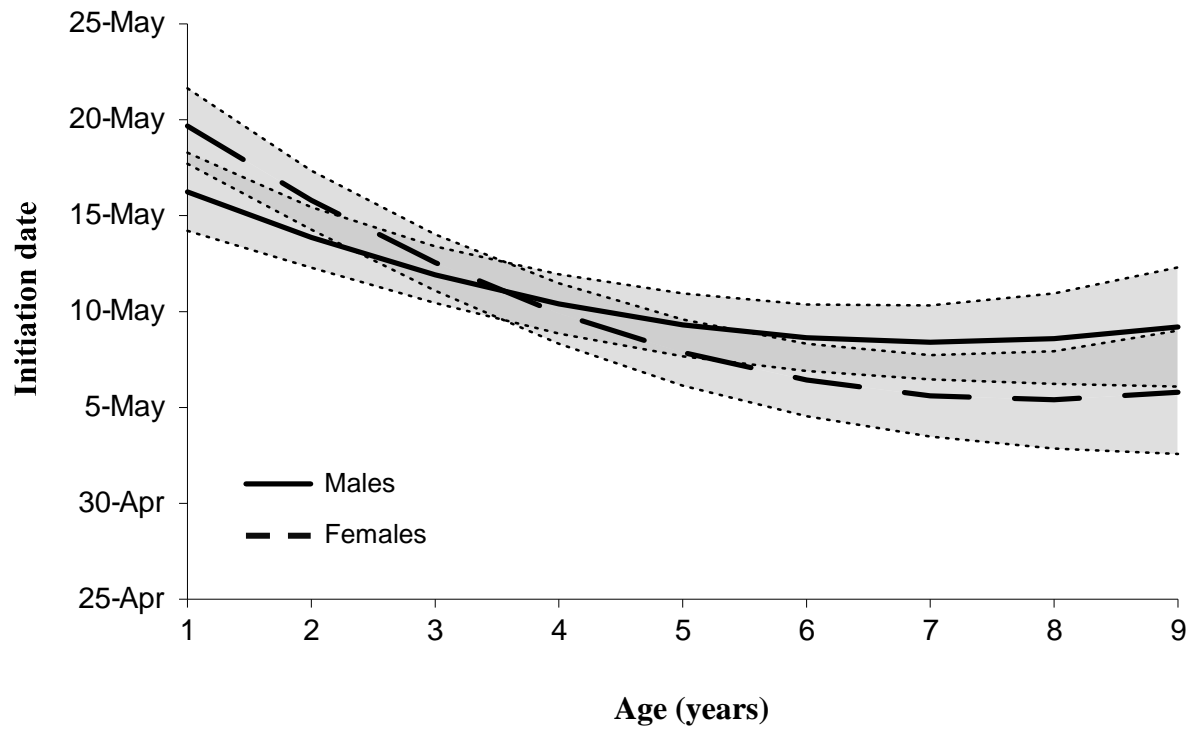


Figure 1. Effects of male and female age on initiation date of first nests of Great Lakes Piping Plovers during 1993-2010. Dotted lines indicate 95% confidence intervals.

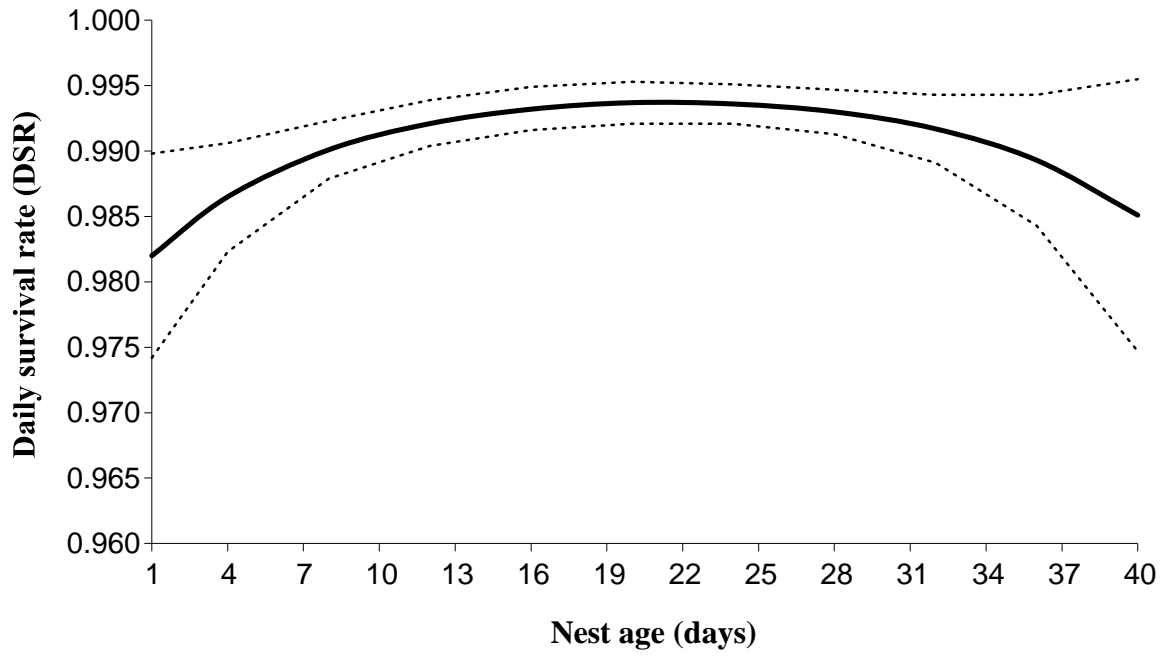


Figure 2. Effect of nest age on daily survival rate (DSR) of Great Lakes Piping Plover nests. Dotted lines indicate 95% prediction intervals. Note that all nests were protected by predator exclosures.

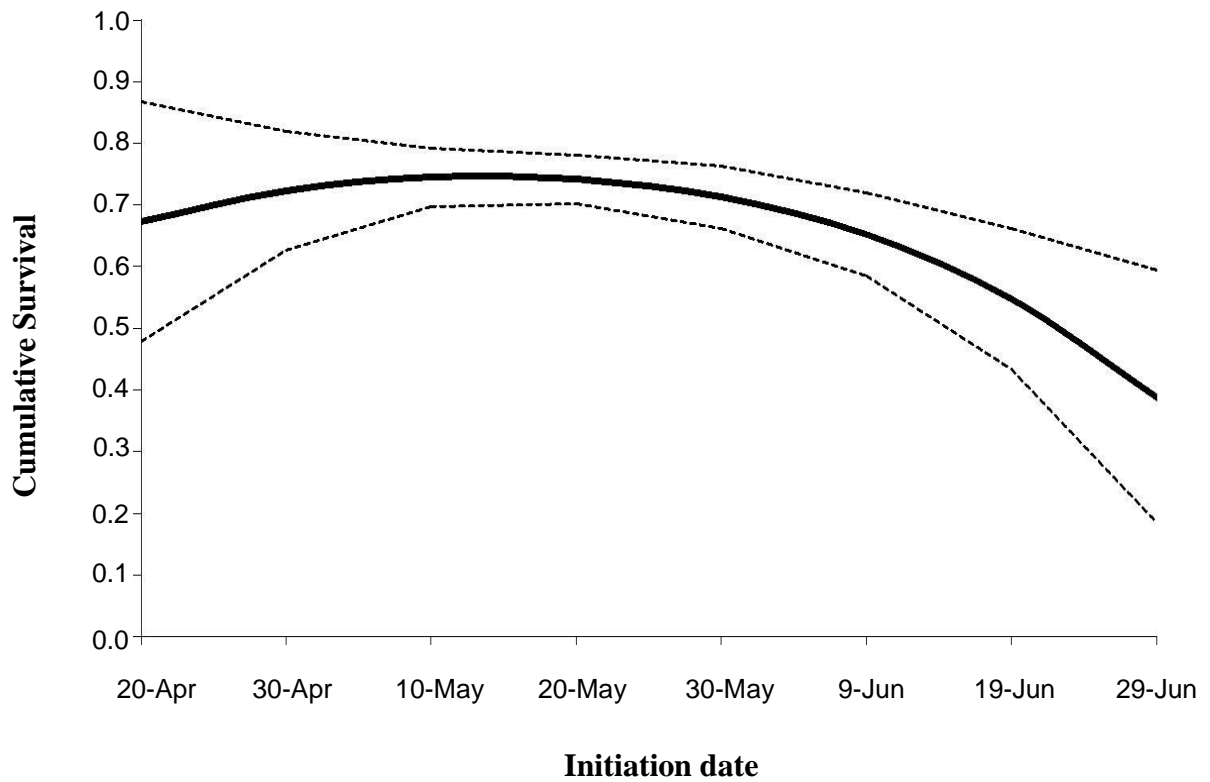


Figure 3. Effect of nest initiation date on cumulative survival of Great Lakes Piping Plover nests for an average 34-day exposure period. Dotted lines indicate 95% prediction intervals. Note that all nests were protected by predator exclosures.

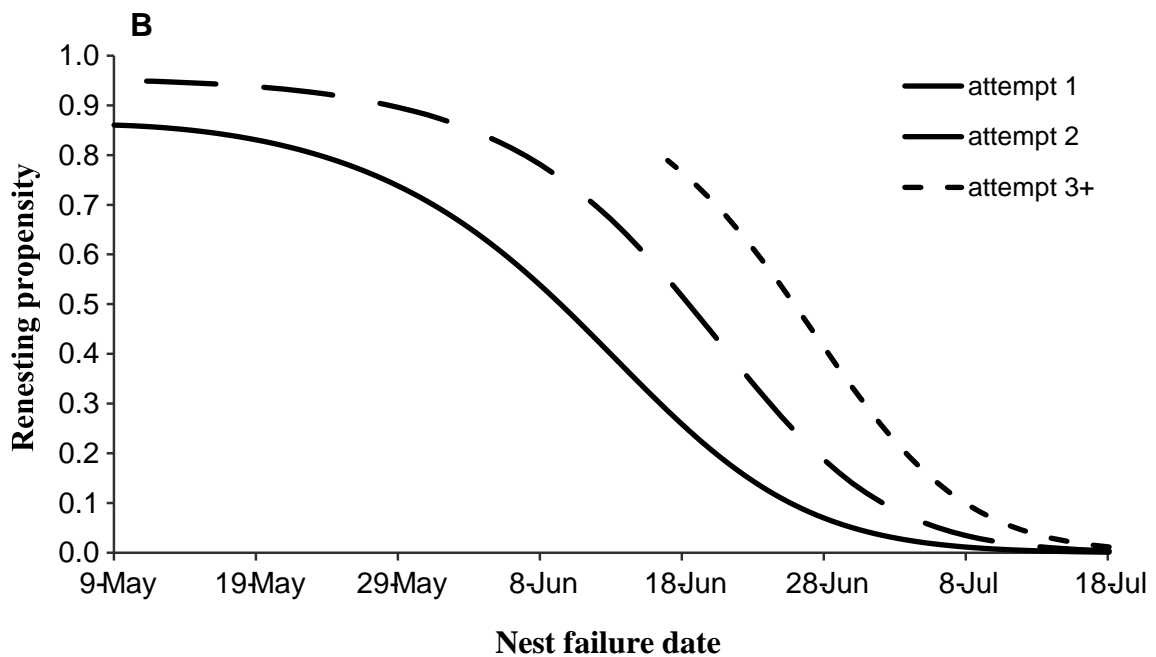
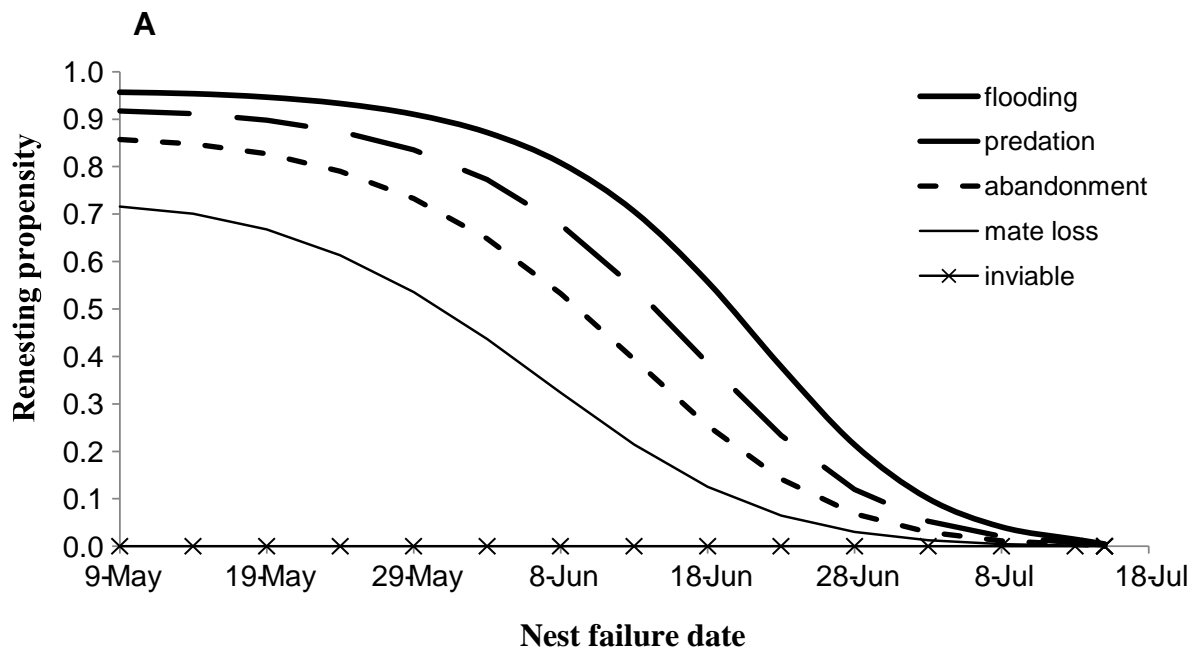


Figure 4. Effects of nest failure date on renesting propensity according to A) cause of nest failure and B) nesting attempt. In plot A, nesting attempt was held to the mean covariate value (1.22), and in plot B, cause of failure was held to the mean covariate value (0.25).

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CHAPTER 2:

Effectiveness of Direct Payments to Increase Reproductive Success of Sandbar-Nesting River Birds in Cambodia

INTRODUCTION

Nesting success, an important metric in avian demographic studies, is often the focus of conservation efforts for declining species (Sutherland *et al.* 2004). Among birds, survival rates of nests and chicks are influenced by a variety of factors, including seasonal effects (Grant *et al.* 2005), predation (Neuman *et al.* 2004), human exploitation (Sok *et al.* 2012), disturbance (Yasué and Dearden 2006), and environmental factors (Smith *et al.* 2007). Recovery of threatened bird species frequently requires mitigation of anthropogenic effects, such as preventing egg harvest (Sok *et al.*) or minimizing detrimental human activities (Burger *et al.* 2004). Conservation becomes more challenging, however, if local human livelihoods are dependent on eggs or chicks for food or trade, or if poverty impedes communities from conserving natural resources (Clements *et al.* 2010). In developing countries, where such circumstances are frequently encountered, voluntary conservation action by local communities may be unrealistic (Gjertsen and Niesten

2010). Thus, incentive-based conservation programs that involve direct payments to individuals or communities have gained in popularity.

Direct payments for biodiversity conservation, which fall under the broad category of payments for ecosystem services (PES), have frequently been used to protect breeding sea turtles (Ferraro and Gjertsen 2009, Gjertsen and Niesten 2010) and more recently, to protect bird nests, especially in Southeast Asia (Sok *et al.* 2012, Clements *et al.* 2013, Wright *et al.* 2013). Because bird and turtle nesting sites can be monitored relatively easily, they are ideally suited for community-based conservation programs involving direct payments. Direct payments offer potential advantages over indirect conservation approaches (e.g., legal-policy interventions, education programs, alternative livelihood development) by being relatively straightforward to implement, cost-effective, and directly focused on a specific conservation outcome such as nesting success (Ferraro 2001). Furthermore, direct payments provide unambiguous incentives to local communities. In the case of bird nest protection, payments deter community members from harvesting eggs, and instead encourage them to protect nests. Yet, compared to the number of direct payment schemes implemented worldwide, there have been few assessments of the effectiveness of direct payment programs. Although direct payment nest protection programs in Cambodia have received some of the most thorough investigation to date (Sok *et al.* 2012, Clements *et al.* 2013, Wright *et al.* 2013), conflicting results highlight the need to further explore this topic.

The Mekong River and its major tributaries (Sekong and Sesan rivers) in northeastern Cambodia and southern Laos contain critical breeding habitat for birds that nest on riverine sand and pebble (shingle) bars. These rivers support regionally important

populations of River Tern *Sterna aurantia*, River Lapwing *Vanellus duvaucelii*, and Great Thick-knee *Esacus recurvirostris* (Thewlis *et al.* 1998, Timmins and Men 1998, Bezuijen *et al.* 2008). As ground-nesting river channel specialists, this group is particularly sensitive to hydrological changes, predation, and disturbance (Timmins and Men 1998, Claassen 2004). Increased anthropogenic threats from human population and economic growth, and subsequent proliferation of large-scale infrastructure developments such as hydropower, intensification of commercial forestry, agriculture, gold mining, increased hunting and disturbance, climate change, and other land-use activities, have led to population declines regionally (Thewlis *et al.* 1998, Claassen 2004, Bezuijen *et al.* 2008) and globally (IUCN 2015). River Tern populations in the Mekong River basin have been especially impacted, having declined by >75% in the last decade (Timmins 2006, Bezuijen *et al.* 2008). The River Tern will likely be the next species to disappear from the region unless focused conservation action is taken (Goes 2013). Furthermore, the Black-bellied Tern *Sterna acuticauda* has already disappeared from the Mekong basin, likely due to the same factors that threaten the River Tern (Goes *et al.* 2010). Despite population declines, riverine sandbar-nesting birds in Southeast Asia have been low priorities for conservation until recently. The lack of conservation attention has, in part, been due to large global ranges and larger populations elsewhere in Asia (IUCN 2015). However, loss of regional populations will significantly shrink species' global ranges and reduce genetic diversity. Thus, it is important to maintain viable regional populations.

To date, few studies have documented the ecology of riverine sandbar-nesting species in Asia. In particular, information on breeding season threats and nesting success are critical to designing effective conservation strategies. Therefore, the objectives of this

study were to investigate factors affecting nest survival, and likelihood of nest predation or egg harvest, for six sandbar-nesting species (River Tern, River Lapwing, Great Thick-knee, Indian Thick-knee, Small Pratincole, and Little Ringed Plover). For the River Tern, we also investigated factors affecting chick survival rates. Additionally, we implemented a direct payment program to increase reproductive success of focal species, especially the River Tern. Specifically, we sought to assess the effectiveness of the direct payment program to improve reproductive rates. This information has important implications for conservation of sandbar-nesting river birds in Southeast Asia, as well as for direct payment for biodiversity conservation programs.

METHODS

Study area and focal species

From 2010-2014, we studied six riverine sandbar-nesting bird species along an approximately 60 km stretch of the Mekong River between Stung Treng (13°32'N, 105°58'E) and Kratie (12°29'N, 106°14'E) towns in northeastern Cambodia (Figure 1). We chose this river stretch because it contains the majority of the populations of key species such as River Terns, River Lapwings, and Great Thick-knees in the Mekong basin (Bezuijen *et al.* 2008). This river stretch ranges from 1-11 km in width and contains approximately 40 permanent islands and hundreds of seasonally emergent sandbars; it has been described in detail by Bezuijen *et al.* (2008). Nesting habitat consisted of sparsely- to moderately-vegetated, seasonally-emergent sand and pebble (shingle) bars.

Our study prioritized River Tern, the species of highest regional conservation concern (Goes 2013); nest searching efforts, nest protection payments, efforts to recruit

community nest protectors, and program awareness-raising activities were highest for this species. Additional focal species included: River Lapwing, Great Thick-knee, Indian Thick-knee, Small Pratincole, and Little Ringed Plover. The latter two species were included despite their low conservation status (Goes 2013, IUCN 2015) because we sought to expand inference to additional species regarding threats and effectiveness of nest protection and to broaden community participation in the program.

Nest monitoring

From 2010-2014, we located and monitored nests during each breeding season (January-May). Nests were located primarily by observing adult behavior. Nest searching focused on River Tern and River Lapwing. We attempted to locate all River Tern nests within the study area. We located as many River Lapwing nests as time allowed, distributing search efforts spatially to minimize effects of pseudoreplication (Hurlbert 1984). Nests of other species were located opportunistically.

Nests were monitored until all eggs hatched or were determined to have failed. Intervals between researcher visits averaged 4.7 ± 3.6 (SD) days. During nest visits, data were collected on nest age, initiation date, fate (success or failure), date of hatch or failure, and cause of failure. Nest age was determined by egg floatation (Westerkov 1950, Hays and LeCroy 1971). Nest initiation date was estimated by back-dating according to nest age, assuming a 1-day laying interval for all species (AHC, personal observation). A nest was considered successful if at least one egg hatched. Nest fates were determined by observations of chicks, nest age, parental behavior, river stage, and signs at the nest such as tracks and eggshell fragments (Mabee 1997).

River Tern chicks were monitored after hatching to assess survival. Chicks left the nest scrape after 1-2 days but remained in the general vicinity until they fledged. Fledging success was based on direct observations of fledged juveniles. Chicks are cryptic and easily overlooked. Therefore, during intermediate site visits, chick survival was assessed from direct observation of chicks or behavior of breeding adults (carrying fish or exhibiting defensive behavior). A brood was considered successful if at least one chick fledged.

Nest protection

A direct payment nest protection program was implemented for focal species; community members were hired to guard nests from potential predators and disturbances. Payment amounts varied among years and species, and were outcome-based, with nest payments varying according to nest fate and cause of failure (Table 1).

In addition to nest guarding, predator exclosures (Smith *et al.* 2011) were used from 2012-2014 to protect a subset (15%) of River Tern nests; nests were selected for exclosure based on logistical feasibility and convenience. Exclosures were erected as soon as possible after locating nests, and remained in place for 2-12 days after chicks hatched (all exclosures were removed prior to fledging). Exclosures consisted of wire-mesh fencing erected around nests and were open on top to allow access by incubating adults. Exclosures were circular, with heights ranging from 0.3-0.5 m, and diameters ranging from 3.2 m (10 m length of fencing) in 2012 to 9.5 m (30 m length of fencing) in 2014; diameter was increased each year to improve adult acceptance rates. Small (2 cm) mesh size prevented access by mammalian predators such as rodents. Following installation, exclosures were monitored for up to two hours to ensure acceptance by

incubating River Terns. Exclosures were removed if adults did not return to nests within the two-hour monitoring period; we waited ≥ 3 days before re-installing exclosures. If adults returned to nests within two hours, exclosures were left in place; however, if a nest remained untended for 24 hours, we considered the nest abandoned due to exclosure installation.

Statistical analyses

We used an information-theoretic approach (Burnham and Anderson 2002) to investigate variation in daily survival rates (DSR) of nests and chicks using the NLMIXED procedure with SAS software (Rotella *et al.* 2004; SAS version 9.4, SAS Institute, Cary, NC). We used a logit link function to constrain DSR to be between zero and one. For ease of interpretation, we converted estimates of DSR into nest success (probability of a nest surviving the entire nesting period) or fledging success (probability of a chick surviving until fledging age) by taking the product of predicted DSR for each day of an average nesting or chick period, using appropriate covariate values for each day (Shaffer and Thompson 2007). If nest fate was ambiguous, we calculated DSR on all intervals prior to age of potential hatch (Stanley 2000). We investigated variation in likelihood of nest failure due to egg harvest by humans or predation by animals using Fisher's exact tests and Chi square (χ^2) tests for trends in proportions using R statistical software (version 3.2.2; Bates *et al.* 2015, R Development Core Team 2015).

For each response variable (nest survival, likelihood of harvest or predation, and chick survival), we investigated variation according to biologically relevant covariates. We investigated whether nest survival varied according to nest age, initiation date, year, site, or level of nest protection. We considered whether likelihood of egg harvest or nest

predation varied according to year or level of nest protection. We examined whether River Tern chick survival varied according to hatching date, chick age, year, site, or level of protection.

We considered day 1 = 1 January and nest age 1 = the day the first egg was laid; we incremented both date and nest age daily. Because we assumed there was variation between years and sites, we included year and site as random effects. We also considered year as a linear trend. Nest protection for River Lapwing, Great Thick-knee, Small Pratincole, and Little Ringed Plover consisted of guarding only; for these species, we treated nest protection as a categorical dummy variable (GUARD; 0 = no protection, and 1 = protection by guarding). For River Terns, a subset of guarded nests and chicks were also protected by exclosures; we therefore considered three different model structures to represent River Tern nest and chick protection: 1) protection as a dummy variable (PROTECT_2; 0 = no protection, and 1 = protection by guarding or exclosure); 2) protection as a discrete variable with 3 levels (PROTECT_3; 0 = no protection, 1 = guarding only, and 2 = guarding plus use of an exclosure), and 3) exclosure as a dummy variable (EXCLOSURE; 0 = no exclosure, and 1 = exclosure).

We used a forward selection approach to model building, starting with the simplest model containing an intercept-only term and sequentially adding variables to each model. First, we considered year and site as a priori random effects and added these effects singly to the intercept-only model. We considered support for a random effect if $p < 0.05$, or $\sigma^2 > 0$ and 95% prediction intervals excluded zero (Zuur *et al.* 2009). Next, we sequentially added fixed effects such as date, age, protection, and year (linear form). We evaluated models by ranking them according to their Akaike's Information Criteria

values adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). If a model under consideration included a main effect (linear term) for date, age, or year, we also considered the quadratic term for that covariate. If two main effects were included in a model, we also considered their interaction. We identified the best-supported model in each candidate set based on the lowest AIC_c value and the largest Akaike weight (w_i), which is the probability of a model being the best in the candidate set (Burnham and Anderson 2002). We considered a model to be competitive if it was ≤ 2 AIC_c units of the best model, as long as it was not merely the best model plus one uninformative parameter (Burnham and Anderson 2002, Arnold 2010). Unless otherwise indicated, means are reported ± 1 standard deviation (SD).

RESULTS

From 2010-2014 we located 772 nests of six species and monitored them for 7,758 exposure days. Small Pratincole nests dominated the sample ($n = 504$ nests; 4,326 exposure days), followed by River Lapwing ($n = 90$ nests; 1,313 exposure days), Little Ringed Plover ($n = 83$ nests; 951 exposure days), River Tern ($n = 79$ nests; 947 exposure days), Great Thick-knee ($n = 14$ nests; 176 exposure days), and Indian Thick-knee ($n = 2$ nests; 45 exposure days). Community nest protectors guarded 92% of River Tern (77% by guarding only, and 15% by guarding plus an enclosure), 54% of River Lapwing, 93% of Great Thick-knee, 100% of Indian Thick-knee, 84% of Small Pratincole, and 54% of Little Ringed Plover nests (Table 1). The average age of nests at discovery was 5.6 ± 4.7 days for River Terns, 13.9 ± 8.8 days for River Lapwings, 10.5 ± 8.7 days for Great Thick-knees, 8.5 ± 2.1 days for Indian Thick-knees, 11.3 ± 7.2 days for Small

Pratincoles, and 8.0 ± 6.0 days for Little Ringed Plovers. For clutches with known initiation and hatching dates, average incubation periods (from day first egg was laid until day first egg hatched) were 23.5 ± 2.6 days for River Terns, 31.0 ± 3.7 days for River Lapwings, 29.0 days for Great Thick-knees, 30.0 ± 2.8 days for Indian Thick-knees, 20.9 ± 3.3 days for Small Pratincoles, and 26.2 ± 3.0 days for Little Ringed Plovers.

Nest survival

Apparent nest success, the proportion of nests that hatched at least one chick, was 47% for River Terns, 56% for River Lapwings, 54% for Great Thick-knees, 100% for Indian Thick-knees, 45% for Small Pratincoles, and 33% for Little Ringed Plovers.

For River Terns, the best-supported model of DSR included an effect of nest protection as a discrete variable with 3 levels (PROTECT_3; Tables 2 and 3). Based on this model, River Tern nest success averaged 0.60 ± 0.12 (SE) for a nest protected by an enclosure plus guarding, 0.29 ± 0.05 (SE) for a nest protected by guarding only, and 0.05 ± 0.05 (SE) for a nest that was not protected (Figure 2).

For River Lapwings, the best-supported model of DSR included a linear effect of year (Tables 2 and 3). Based on this model, River Lapwing nest success declined during the study, from 0.65 ± 0.10 (SE) in 2010 to 0.17 ± 0.08 (SE) in 2014.

For Small Pratincoles, the best-supported model of DSR included an effect of nest age, a linear year effect, and effects of nest initiation date and nest protection (Tables 2 and 3). Based on this model, Small Pratincole nest success increased with nest age, from 0.19 ± 0.02 (SE) for a 1-day-old nest to 0.96 ± 0.01 (SE) for a 21-day-old nest that was about to hatch. Also, nest success declined over the study, from 0.51 ± 0.06 (SE) in 2010 to 0.07 ± 0.02 (SE) in 2014 (Figure 3). Additionally, nest success declined from $0.43 \pm$

0.07 (SE) for early-season nests (6 January) to 0.05 ± 0.02 (SE) for late season nests (8 May). Finally, Small Pratincole nest success averaged 0.21 ± 0.03 (SE) for guarded nests and 0.06 ± 0.03 (SE) for unguarded nests (Figure 3).

For Little Ringed Plovers, the best-supported model of DSR included an effect of nest initiation date (Tables 2 and 3). Based on this model, Little Ringed Plover nest success declined with later nest initiation, from 0.68 ± 0.11 (SE) for early-season nests (January 21) to 0.01 ± 0.01 (SE) for late-season nests (21 April). We did not model DSR for Great or Indian Thick-knees due to small sample sizes.

Causes of nest failure

River Tern nest failures ($n = 43$) were caused by predation by animals (47%), egg harvest by humans (26%), abandonment (16% [7% due to enclosure installation; 2% due to the apparent death of the incubating adult by an aggressive Brahminy Kite *Haliastur indus*; 7% due to other non-investigator related reasons]), flooding (5%), cracked eggs (5%), and trampling by domestic water buffalo (2%). River Lapwing nest failures ($n = 39$) were caused by animal predation (67%), egg harvest by humans (23%), inundation (5%), trampling by water buffalo (3%), and egg inviability (3%). All Great Thick-knee nest failures ($n = 6$) were caused by animal predation (100%). Small Pratincole nest failures ($n = 258$) were caused by animal predation (69%), egg harvest by humans (15%), abandonment (9% [3% due to heavy rain, 1% due to apparent predation on adults by Peregrine Falcons *Falco peregrinus*, and 5% due to other non-investigator related reasons]), inundation (4%), trampling by water buffalo (3%), and cracked eggs (1%). Little Ringed Plover nest failures ($n = 56$) were caused by animal predation (61%), egg harvest by humans (25%), inundation (7%), abandonment (5% [1% due to extreme heat;

4% due to other non-investigator related reasons]), and cracked eggs (2%). Both Indian Thick-knee nests were successful.

Predation by animals was the leading cause of nest failure, accounting for 65% of nest failures for all species pooled. Predator species could be accurately identified from direct observation or clear signs in 19% of nest predation cases, probable predator species was inferred based on some evidence in 36% of cases, and predator species was unknown in 45% of cases. Rats (captured individuals were provisionally identified as Asian House Rat *Rattus tanezumi*) were the primary nest predators of River Terns, Great Thick-knees, and Little Ringed Plovers. Southern Jungle Crow *Corvus macrorhynchos* was the primary nest predator of River Lapwings and Small Pratincoles. Other nest predators included domestic dog, domestic chicken, and Little Heron *Butorides striata*. Additionally, Great Thick-knees and River Lapwings destroyed four nests of other species. Predation increased over the course of the study for all species pooled ($\chi^2 = 38.94$, $df = 1$, $P < 0.001$; Figure 4). A significant increase in nest predation occurred during the 2010-2011 period (Fisher's exact test odds ratio (OR) = 2.12, $P = 0.04$), but not during 2011-2012 (OR = 0.69, $P = 0.32$), 2012-2013 (OR = 0.89, $P = 0.58$), or 2013-2014 (OR = 0.86, $P = 0.53$). From 2010-2014, the proportion of predated clutches increased for River Lapwings ($\chi^2 = 11.32$, $df = 1$, $P < 0.001$), Small Pratincoles ($\chi^2 = 23.14$, $df = 1$, $P < 0.001$) and Little Ringed Plovers ($\chi^2 = 10.65$, $df = 1$, $P = 0.001$), but not River Terns ($\chi^2 = 1.39$, $df = 1$, $P = 0.24$) or Great Thick-knees ($\chi^2 = 1.81$, $df = 1$, $P = 0.18$).

Egg harvest by humans was the second leading cause of nest failure, accounting for 18% of nest failures for all species pooled. Clutches were harvested by adults (67%) and children (33%). Egg harvest decreased over the course of the study for all species

pooled ($\chi^2 = 9.10$, $df = 1$, $P = 0.003$; Figure 4). The likelihood of egg harvest decreased significantly during the 2010-2011 (OR = 2.12, $P = 0.04$) and 2011-2012 periods (OR = 3.38, $P = 0.01$), but not during 2012-2013 (OR = 0.45, $P = 0.16$) or 2013-2014 (OR = 0.70, $P = 0.54$). Over the course of the five-year study (2010-2014), the proportion of harvested clutches decreased for River Terns ($\chi^2 = 6.68$, $df = 1$, $P = 0.009$) and River Lapwings ($\chi^2 = 8.21$, $df = 1$, $P = 0.004$), but not Small Pratincoles ($\chi^2 = 1.41$, $df = 1$, $P = 0.23$) or Little Ringed Plovers ($\chi^2 = 1.15$, $df = 1$, $P = 0.28$). For River Terns, 50% of unprotected clutches ($n = 6$), 11% of guarded clutches ($n=64$), and 0% of exclosed clutches ($n = 7$) were harvested by humans. The proportion of harvested River Tern clutches was significantly lower for protected than unprotected nests ($\chi^2 = 6.68$, $df = 1$, $P = 0.009$). The proportion of clutches that were harvested was also significantly lower for protected nests of Small Pratincoles (OR = 2.98, $P = 0.007$) and Little Ringed Plovers (OR = 4.39, $P = 0.04$). Nest protection did not significantly reduce harvest of River Lapwing clutches (OR = 1.22, $P = 1$).

River Tern chick survival

Of 44 River Tern broods that were monitored for the entire chick period, apparent brood success (proportion of broods where at least one chick fledged) was 47%. The average exposure period for chicks was 14.7 ± 8.2 days. For five broods with known fledging dates, the average chick period was 22.0 ± 1.3 days. Of 8 broods protected by exclosures, 100% were released prior to fledging; the average length of time broods were kept inside exclosures was 8.0 ± 2.9 days. The best-supported model of River Tern chick survival included protection as a discrete variable with three levels (PROTECT_3) and hatch date (Tables 2 and 3). Based on this model, River Tern chick survival declined during the

course of the breeding season, and varied according to level of nest protection, with survival rates being highest for chicks protected by exclosures and lowest for unprotected chicks (Figure 5). River Tern fledging success was 0.82 ± 0.14 (SE) for chicks that were protected by exclosures and nest guarding, 0.40 ± 0.09 (SE) for chicks that were guarded only, and 0.02 ± 0.05 (SE) for unprotected chicks.

DISCUSSION

Direct payment programs have frequently been used to protect threatened birds (Sok *et al.* 2012, Clements *et al.* 2013, Wright *et al.* 2013) and turtles (Ferraro and Gjertsen 2009, Gjertsen and Niesten 2010). In Cambodia, direct payments for bird nest protection have been effective for some species (Clements *et al.* 2013), but equivocal for others (Sok *et al.* 2012, Wright *et al.* 2013). Although Sok *et al.* (2012) included the same population of River Terns in their analysis and found little evidence that nest protection was effective, shortcomings of their study were: unguarded control nests were lacking, nest protection was not included as a covariate in the analyses, and nest data were limited to 2011, a year when exclosures were not tested. The current study provides a more comprehensive assessment of the effectiveness of nest protection for River Terns in Cambodia.

Overall, our results indicate that the direct payment nest protection program was effective in reducing egg harvest and increasing reproductive success rates. The program was most beneficial for River Terns, the species of highest conservation concern and primary focal species of the program. In addition to nest guarding, the use of exclosures was an integral component of River Tern nest and chick protection. An exclosed (and

guarded) River Tern nest was 2.1 times more likely to be successful than a nest that was guarded only, and 11.0 times more likely to be successful than an unprotected nest (Figure 2). Furthermore, a River Tern brood that was protected by an enclosure was 2.1 times more likely to successfully fledge than a brood that was guarded only, and 52.8 times more likely to fledge than an unprotected brood (Figure 5). Nest protection also improved Small Pratincole nest success; a guarded nest was 3.3 times more likely to succeed than an unguarded nest (Figure 3). Nest protection was especially effective at reducing rates of egg harvest by humans. The decline in egg harvest corresponded to the general pattern of stronger nest protection program management and implementation in each successive year of the study. During the first year (2010), nest protection was implemented on a small scale, and without a community awareness component. With support from the Worldwide Fund for Nature (WWF – Cambodia program), the program was expanded considerably in the second year (2011) and included educational awareness to communities regarding the program; WWF support continued for the duration of this study and community awareness and participation increased during each successive year. Despite having a stronger program, a slight increase in egg harvest occurred in 2013 and 2014 (Figure 4); however, the majority of harvested nests during those years were from unprotected sites.

Nest guards were frequently recruited from among the primary resource users (e.g., fishers, farmers) at each breeding location. By enlisting their participation in the nest protection program, these resource users (as well as their extended families) were therefore effectively removed from the pool of potential egg harvesters. To our knowledge, no nests were harvested by any nest guard or member of their extended

families. In fact, nest guards became program advocates; they spread awareness of the program and frequently recruited additional nest protectors from among their extended families and communities. All cases of egg harvest occurred when nest protectors were absent from their guard posts; although nest protectors were supposed to guard nests at all times, they occasionally left their posts. However, in one case, a nest guard was able to retrieve a stolen River Tern clutch and return the eggs to the nest, where they later successfully hatched. In another incident, nest guards retrieved two stolen White-shouldered Ibis *Pseudibis davisoni* chicks and reunited them with their parents (concurrent WWF nest protection program; Sok *et al.* 2012); meanwhile, they assisted the ibis chick thief to locate and protect a River Tern nest.

Despite the effectiveness of the nest protection program to reduce egg harvest, the program was less effective against animal predation. Predation, especially by rats and Southern Jungle Crows, increased significantly over the course of the study. In the first year (2010), egg harvest was the primary cause of nest failure, but by the second year (2011), predation surpassed egg harvest as the primary cause of nest failure (Figure 4). The likelihood of nest predation was especially high during the last three years of the study (2012-2014). This pattern of nest predation mirrored observed frequencies of rats and crows in the study area; on average, rat signs and crows were observed once per week during 2010-2011, but sightings increased to several per day during 2012-2014. Nest predation rates and the frequency of predator observations also corresponded to regional weather patterns during the study. 2010 was an especially dry year, but was followed by higher than average rainfall in 2011 and consequent widespread flooding along the Mekong River. Observations of rat signs and crows increased in the following

breeding season of 2012, and nest predation rose during that year. The frequency of rat signs and crow sightings, as well as nest predation rates, remained high during subsequent years of the study. Studies of other systems have documented positive effects of precipitation and weather events on rodents and birds (Madsen and Shine 1999, Jaksic 2001). We speculate that rat and crow populations increased in the study area due to increased food resources following the 2011 rains and floods. Higher than average rainfall may have led to increased primary (vegetation) or secondary (arthropod) production (Jaksic 2001), or possibly, detritus that remained after flood waters receded was more abundant than in average rainfall years, benefitting opportunistic scavengers such as rats and crows. In 2016, a drought year, a sharp decline in the rat (but not crow) population occurred such that the frequency of rat signs was similar to pre-2011 levels (AHC, personal observation), providing further anecdotal evidence that precipitation, or a lack thereof, is an important driver of rat population trends.

Nest predation posed a significant threat to sandbar-nesting birds in this study. We recommend that future conservation programs for these species increase efforts to mitigate threats from nest predation. Exclosures significantly increased nest and chick survival of River Terns (Figures 2 and 5). Their use should be an essential component of future conservation measures for this species. However, using exclosures required considerable effort and care, including timely delivery of exclosure materials to nesting sites. Ensuring that exclosure installation did not lead to nest abandonment proved to be especially challenging. Following 5 of 15 installations, exclosures had to be removed because incubating adults did not return to their nests. River Terns abandoned 3 of 10 nests, even though adults briefly visited these nests after exclosure installation and we

mistakenly assumed acceptance by the adults. To minimize the risk of nest abandonment, conservation staff and nest protectors should receive comprehensive training in proper set-up and monitoring of exclosures. Also, we recommend that larger exclosures be used in the future to minimize abandonments. When adults did accept exclosures and resumed tending their nests, nest and chick survival was 100%; exclosures were completely effective against predation and no mortality of eggs or chicks occurred within exclosures. Although exclosures were designed to deter rodents, they may also have been visual, if not physical, deterrents to avian predators. Unfortunately, all chicks were released from exclosures prior to fledging, and only 64% of chicks released from exclosures survived to fledging age. To increase the chances of successful fledging, we recommend that River Tern chicks be kept inside exclosures until they fledge; importantly, this will require providing chicks with shade and water. In addition to River Terns, exclosures could potentially be used to protect nests of other species; however, exclosure design and implementation should consider the unique behavior of each species. Additionally, future conservation activities may warrant removal of nest predators, especially seasonal eradication of rats from key River Tern breeding sites. Predator removal measures should integrate into existing community nest protection activities. For example, community nest protectors could also assist with predator removal activities.

Research activity can potentially cause lower nesting success due to increased detection rates by predators (Carney and Sydeman 1999). We therefore took precautions to minimize predation risk, such as postponing nest checks when predators were present and varying approach routes to nests. While exclosed nests were effectively protected from predators, it is possible that predation risk increased for other nearby unfenced

nests. Another potential risk was that nest protector encampments may have attracted predators such as rats and crows. However, encounter rates of rat signs and crows were similar for sites with and without human encampments, suggesting that encampments were not the sole factor influencing predator distribution and abundance. Moreover, a sharp decline in the rat population occurred in 2016, despite the continued presence of nest protector encampments. At most sites, human encampments existed before the nest protection program began; however, prior to the program, inhabitants of encampments were harvesting nests rather than protecting them. Our results, which show that nest protection activities significantly improved nesting success, suggest that these activities were warranted despite the additional disturbance to nesting birds.

As well as nest protection, reproductive success was influenced by seasonal and age effects. Small Pratincole and Little Ringed Plover nest survival declined with later initiation date (Table 3), and River Tern chick survival declined with later hatching date (Figure 5). Seasonal declines in reproductive success have been documented for a wide range of species, and may result from decreased food resources (Verhulst and Nilsson 2008), variation in predator dynamics or environmental conditions (Grant *et al.* 2005), decreased physical condition of breeding adults (Arnold *et al.* 2004), or end-of-season time constraints (Verboven and Visser 1998). For Small Pratincoles, nest survival was also influenced by nest age; older nests had higher survival than younger nests. Studies of other species have documented similar patterns of survival according to nest age (Klett and Johnson 1982, Grant *et al.* 2005), presumably because the most vulnerable nests failed at a young age. In this study, older nests may have survived longer due to nest site characteristics that made them less vulnerable to harvest, predation, or flooding.

Our results illustrate that direct payments to individuals can be an effective tool for species conservation, at least in terms of biological indicators of success; however, direct payment programs also have social implications. Direct payments may create or exacerbate negative social dynamics which can undermine program effectiveness (Sok *et al.* 2012, Clements *et al.* 2013). Furthermore, direct payment initiatives require social responsibility on the part of the payer, and may require taking an adaptive management approach to negotiating with communities (Milne and Niesten 2009). Although our study did not address social implications per se, we suspect that the nest protection program's effectiveness in terms of biological outcomes was influenced by how social aspects were handled. The nest protection program took an adaptive approach to implementing and disbursing nest payments. Nest payment amounts were assessed annually and adjusted when necessary to ensure that nest protectors were fairly compensated for their time, effort, and travel costs, especially considering the high rates of nest predation and consequent pay reductions. Occasionally, discrepancies regarding nest outcomes arose between nest protector reports and research team observations. In such cases, to minimize potential conflicts, nest protectors were given the benefit of the doubt and payments were made in their favor; thus, the burden of proof was borne by the program rather than the individual nest protectors. To reduce the potential for nest protectors to abuse the program by providing false information in anticipation of higher payments, we implemented regular monitoring (of nests and nest protectors), and explained to nest protectors how egg floatation methods allowed us to predict hatching dates. We speculate that the nest protection program's emphasis on creating and maintaining positive relationships with participating community members led to higher program satisfaction

and job performance among nest protectors and therefore indirectly contributed to improved reproductive success rates of the target bird species.

Our results clearly demonstrate that nest protection combined with predator exclosures are highly effective at increasing nest success of River Terns and other sandbar-nesting bird species, and are essential for the survival of these species in the Mekong basin. However, the effectiveness of the direct payment nest protection program was contingent upon having specific and measurable biological indicators, regular monitoring, ability of nest protectors to prevent egg harvest by humans, proper training and use of exclosures to protect nests and chicks from animal predators, and positive relationships between the program and nest protectors. This study illustrates that multiple biological and social factors should be considered when designing and implementing a direct payment initiative, and can affect program success. However, these factors are important in any conservation approach. Our study indicates that direct payments can indeed be a useful tool for biodiversity conservation, especially in developing countries where voluntary conservation action by local communities is unrealistic.

Table 1. Community bird nest protection payments (USD) and proportion of nests that were protected on the Mekong River, Cambodia (2010-2014).

Species	2010	2011	2012	2013	2014
River Tern					
Finder's fee	\$2.5	\$10	\$10	\$10	\$10
Daily fee (successful) ¹	-	\$4	\$4	\$4	\$4
Daily fee (failure; "unpreventable" cause) ^{1,2}	-	\$0	\$1	\$2	\$2
Daily fee (failure; eggs harvested by humans) ¹	-	\$0	\$0	\$0	\$0
Chick bonus	\$2.5	\$8	\$10	\$10	\$10
Proportion of nests that were guarded only	7/11	15/15	20/23	8/8	11/22
Proportion of nests that were guarded + exclosed	0/11	0/15	3/23	0/8	9/22
River Lapwing					
Finder's fee	\$2.5	\$1	\$1	\$1	\$2.5
Chick bonus ³	\$2.5	\$1	\$1	\$1	\$2.5
Proportion of nests that were guarded	3/11	7/20	9/22	7/11	23/26
Great Thick-knee					
Finder's fee	\$2.5	\$2.5	\$2.5	\$2.5	\$2.5
Daily fee ⁴	-	-	-	-	\$1
Chick bonus ³	\$2.5	\$2.5	\$2.5	\$2.5	\$2.5
Proportion of nests that were guarded	1/1	2/2	1/1	4/4	5/6

Indian Thick-knee

Finder's fee	\$2.5	\$2.5	\$2.5	\$2.5	\$2.5
Daily fee ⁴	-	-	-	-	\$1
Chick bonus ³	\$2.5	\$2.5	\$2.5	\$2.5	\$2.5
Proportion of nests that were guarded	0/0	0/0	0/0	1/1	1/1

Small Pratincole

Finder's fee	-	\$0.25	\$0.25	\$0.25	\$0.50
Chick bonus	-	\$0.25	\$0.25	\$0.25	\$0.50
Proportion of nests that were guarded	0/41	80/88	105/121	104/108	133/146

Little Ringed Plover

Finder's fee	-	\$0.25	\$0.25	\$0.25	\$0.50
Chick bonus	-	\$0.25	\$0.25	\$0.25	\$0.50
Proportion of nests that were guarded	0/20	15/27	19/24	4/4	7/8

¹ Payment per person; two people were hired per nest.

² All nest failures were considered “unpreventable” except those caused by harvesting by people.

³ Payment amounts were per chick, except in 2010 when payment amounts were per nest if at least one chick hatched.

⁴ Payment per nest.

Table 2. Best-supported models of clutch size, daily nest survival (DSR), and daily chick survival of sandbar-nesting birds on the Mekong River, Cambodia (2010-2014)

Model ^a	ΔAIC_c^b	w_i^c	K^d	Dev ^e
DAILY NEST SURVIVAL RATE (DSR)				
River Tern ($n = 115$)				
PROTECT_3	0.0	0.47	2	301.4
EXCLOSURE	0.8	0.31	2	302.2
Intercept only	2.6	0.13	1	308.7
AGE ²	4.2	0.06	3	300.7
AGE	5.0	0.04	2	306.3
River Lapwing ($n = 120$)				
YEAR	0.0	0.86	2	213.5
Intercept only	4.3	0.10	1	221.6
IDATE	8.1	0.015	2	221.2
AGE	8.2	0.014	2	221.5
GUARD	8.3	0.013	2	221.6
Small Pratincole ($n = 610$)				
AGE + YEAR + IDATE + GUARD	0.0	0.86	5	967.5
AGE + YEAR + IDATE	3.6	0.14	4	974.7
AGE + YEAR	19.3	0.0001	3	993.9
AGE + IDATE	24.6	0	3	999.2
AGE	34.6	0	2	1012.8
Intercept only	59.0	0	1	1040.8
Little Ringed Plover ($n = 120$)				
IDATE	0.0	0.97	2	193.4
YEAR	7.0	0.03	2	200.2
Intercept only	14.8	0.001	1	211.6
GUARD	16.7	0.0002	2	209.7
AGE	17.9	0.0001	2	210.9
DAILY CHICK SURVIVAL RATE				
River Tern ($n = 53$)				
PROTECT_3 + HDATE	0.0	0.97	2	193.4
PROTECT_3	7.0	0.03	2	200.2

HDATE	14.8	0.001	1	211.6
Intercept only	16.7	0.0002	2	209.7
EXCLOSURE	17.9	0.0001	2	210.9

^a The top five models, plus intercept-only model if not among the top five models, are presented for each set of analyses. Best-supported models in each candidate set are indicated in bold. Fixed effects included nest age (AGE), nest initiation date (IDATE), hatch date (HDATE), year as a linear trend (YEAR), and nest protection; nest protection was considered as a discrete variable with three levels (PROTECT_3) or categorical dummy variables for nest guarding (GUARD) or use of an enclosure (EXCLOSURE). ² indicates a quadratic effect. Sample sizes (*n*) indicate number of intervals for DSR and chick survival analyses.

^b The difference in AIC_c value between the model and the best-supported model.

^c Akaike weight.

^d Number of model parameters.

^e Model deviance.

Table 3. Parameter estimates, standard errors, and 95% confidence intervals for best-supported models of daily nest survival (DSR) and daily chick survival of sandbar-nesting birds on the Mekong River, Cambodia (2010-2014)

Parameter ^a	Estimate	SE	95% Confidence Interval	
			Lower	Upper
DAILY NEST SURVIVAL RATE (DSR)				
River Tern				
INTERCEPT	2.046	0.358	1.337	2.755
PROTECT_3	0.891	0.333	0.231	1.550
River Lapwing				
INTERCEPT	4.644	0.487	3.680	5.608
YEAR	-0.364	0.130	-0.622	-0.107
Small Pratincole				
INTERCEPT	3.457	0.344	2.782	4.132
AGE	0.053	0.012	0.029	0.077
YEAR	-0.330	0.060	-0.447	-0.213
IDATE	-0.011	0.003	-0.016	-0.006
GUARD	0.605	0.220	0.172	1.037
Little Ringed Plover				
INTERCEPT	4.826	0.581	3.676	5.975
IDATE	-0.029	0.007	-0.043	-0.016
DAILY CHICK SURVIVAL RATE				
River Tern				
INTERCEPT	3.321	1.178	0.959	5.684
PROTECT_3	1.576	0.800	-0.029	3.181
HDATE	-0.022	0.010	-0.042	-0.001

^a Model parameters included nest age (AGE), nest initiation date (IDATE), hatch date (HDATE), year as a linear trend (YEAR), and nest protection; nest protection was a discrete variable with three levels (PROTECT_3), or a categorical dummy variable for nest guarding (GUARD).

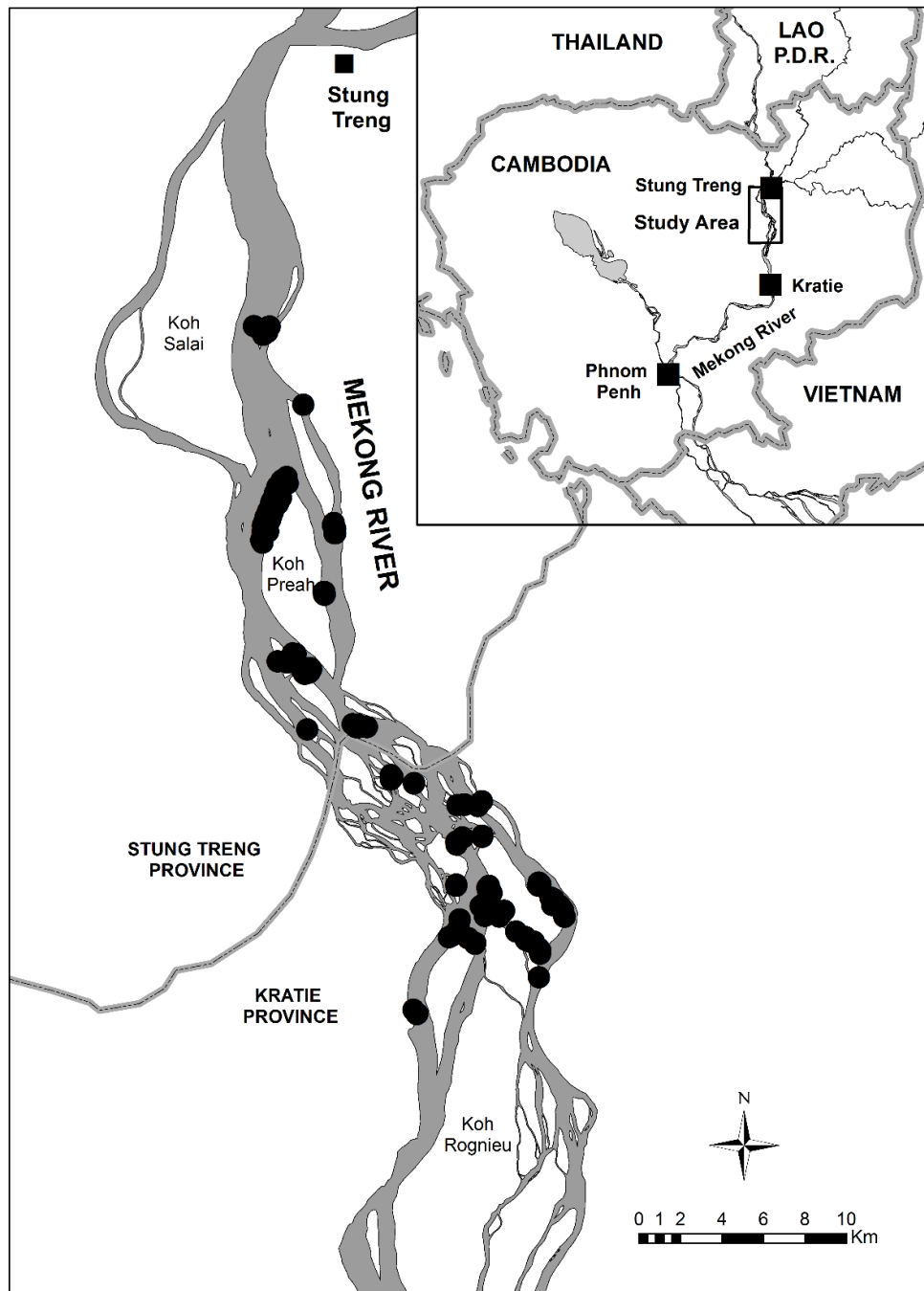


Figure 1. Location of the study area in Cambodia. Black circles represent nest sites that were monitored (2010-2014).

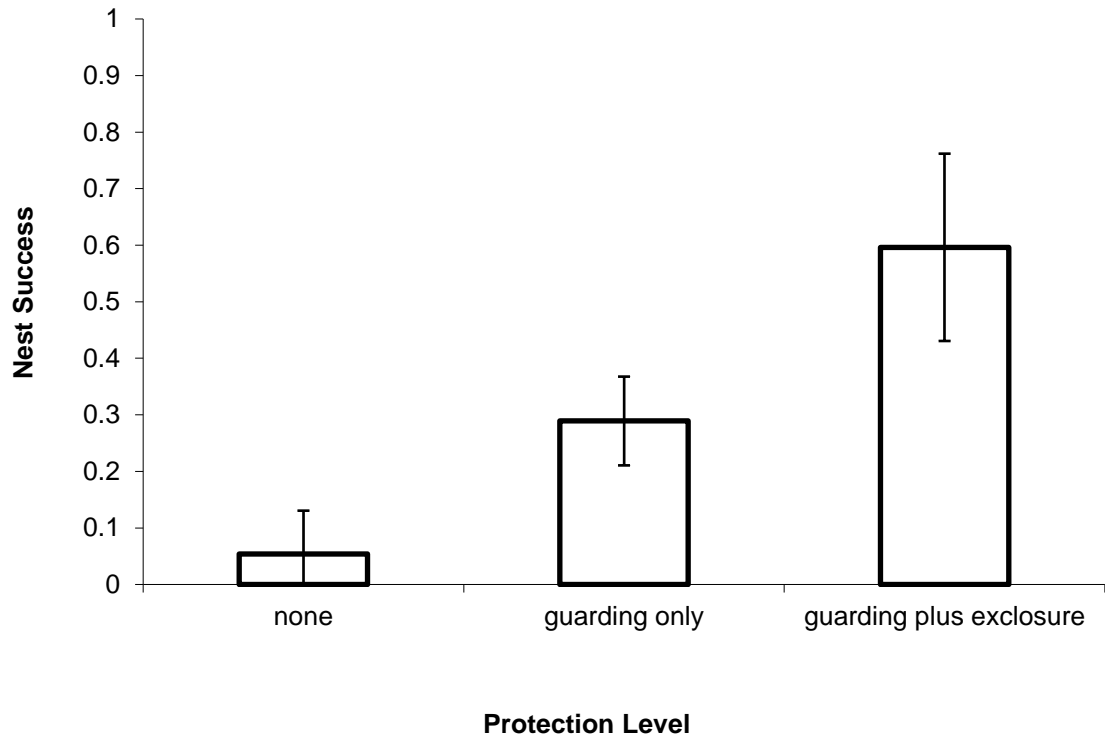


Figure 2. Predicted effect of nest protection on River Tern nest success on the Mekong River, Cambodia (2010-2014). Error bars indicate 85% prediction intervals.

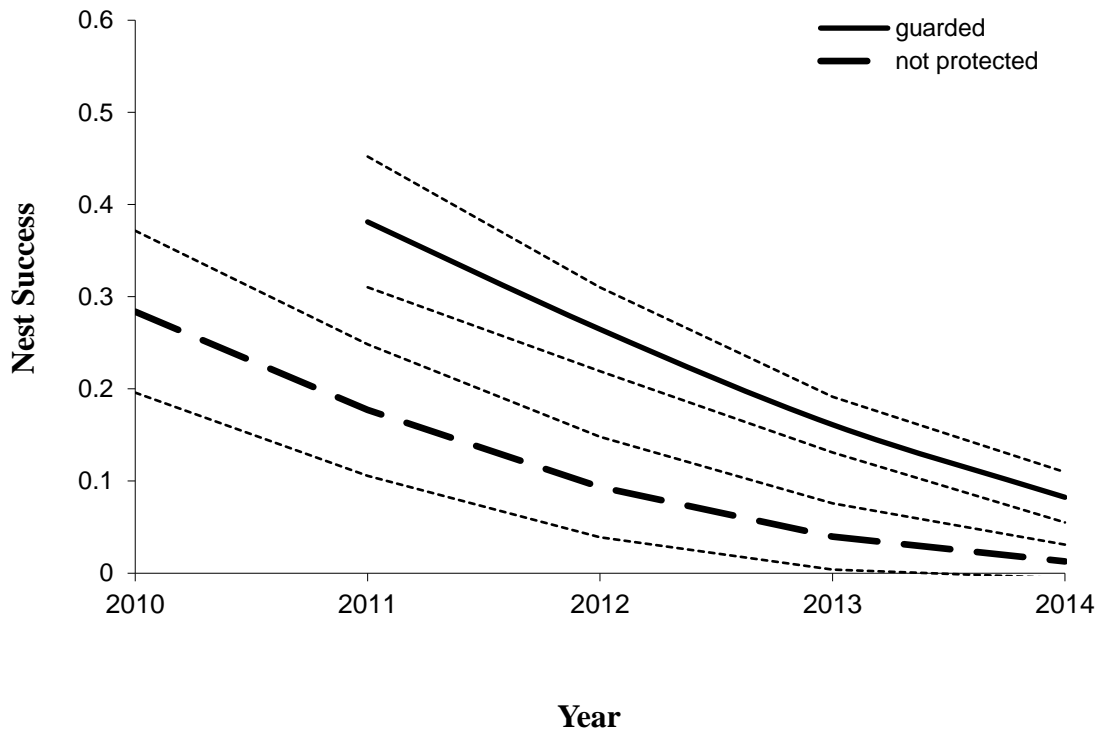


Figure 3. Predicted effects of nest protection and year on Small Pratincole nest success on the Mekong River, Cambodia (2010-2014). Other model covariates were held constant at their mean observed values: nest age = 11.3 days, and nest initiation date = 12 March. Thin dotted lines indicate 85% prediction intervals.

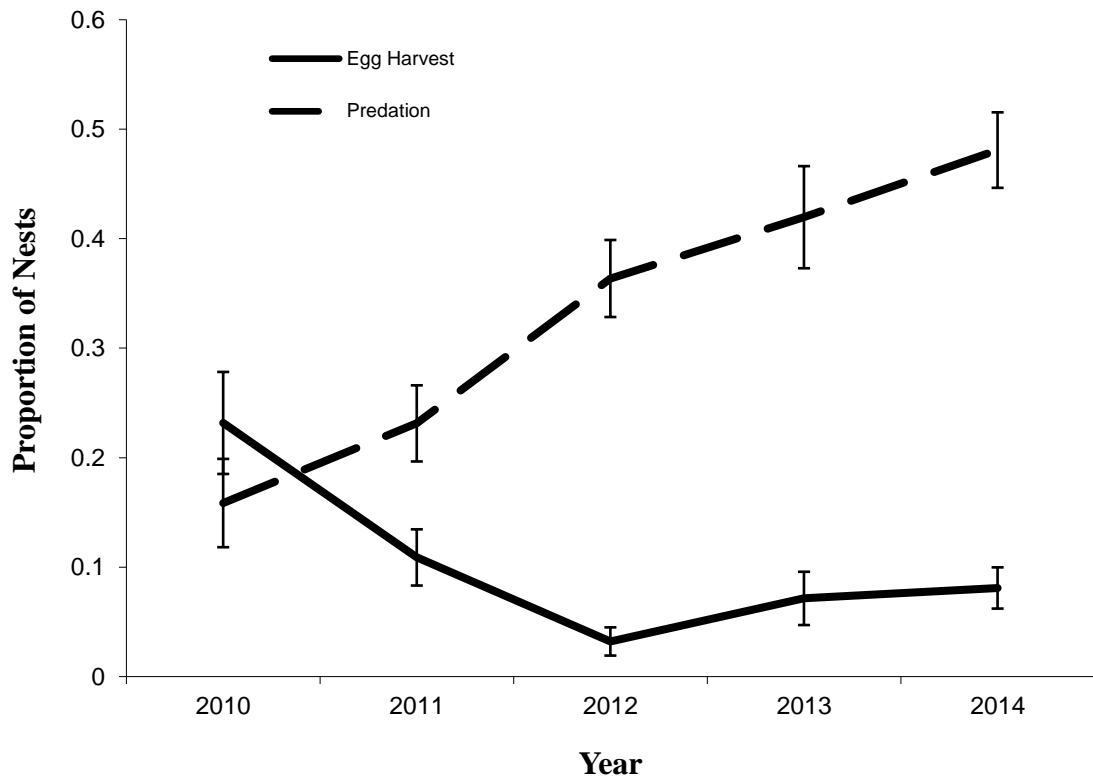


Figure 4. Proportion of nests that failed due to egg harvest by people (solid line) and predation by animals (dashed line) of sandbar-nesting birds on the Mekong River, Cambodia (2010-2014). Nests were pooled for all focal species. Error bars indicate 95% confidence intervals.

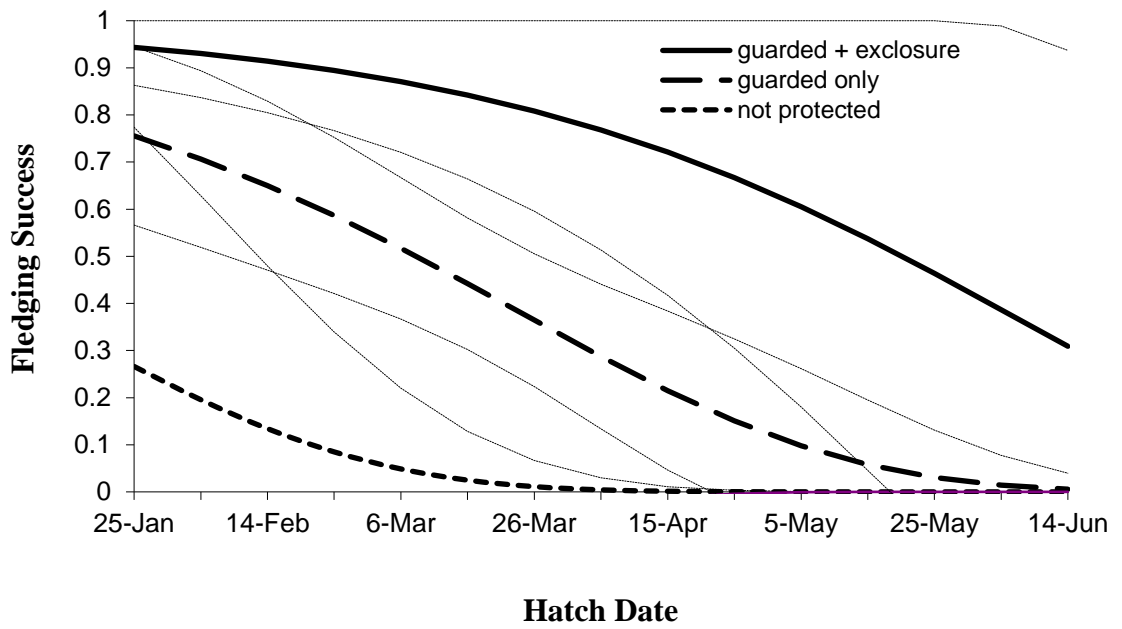


Figure 5. Predicted effects of nest protection and hatching date on River Tern fledging success on the Mekong River, Cambodia (2010-2014). Thin dotted lines indicate 85% prediction intervals.

CHAPTER 3:

Consequences of Multi-Scale Habitat Selection on Reproductive Success of Riverine Sandbar-Nesting Birds in Cambodia

INTRODUCTION

Ecological processes may act on multiple spatial and temporal scales to influence animal behavior and fitness (Senft et al. 1987, Wiens 1989, Orians and Wittenberger 1991).

Because animals select different habitat features at different scales, many habitat selection studies have incorporated multiple spatial scales (Kie et al. 2002, Bonnot et al., 2009, Mayor et al. 2009). However, fewer studies have investigated how habitat selection at multiple spatial scales affects demographic processes. In birds, nest success is an important measure of productivity and identifying factors that affect nest success is often the focus of avian research (Dinsmore et al. 2002, Grant et al. 2005). Many studies of avian nesting success have examined how habitat characteristics at a single scale of selection, such as at the nest site, affect nesting success; however, nesting success may be affected by habitat selection at multiple spatial scales (Cornell and Donovan 2010).

Because birds are assumed to select habitat hierarchically, from coarser to finer scales (Johnson 1980, Jones 2001), habitat selection at larger spatial scales constrains the availability of habitat features at smaller spatial scales (Johnson 1980, Battin and Lawler 2006). At smaller spatial scales, (e.g., local or nest-site scales), habitat selection can affect nesting success due to heterogeneity in visibility or predation risk among potential breeding sites (Magaña et al. 2010, Massaro et al. 2013).

Birds should select breeding habitat that maximizes their reproductive success (Clark and Shutler 1999, Chalfoun and Schmidt 2012). Indeed, adaptive nest-site selection has been indicated for a number of avian species (Martin 1998, Liebezeit and George 2002, Sergio et al. 2003). However, other studies have documented apparent maladaptive selection, whereby habitat features that were selected for had negative effects on nesting success (Misenhelter and Rotenberry 2000, Shochat et al. 2005, Gilroy et al. 2011). Such mismatches between habitat selection and habitat quality indicate the existence of “attractive sinks” or “ecological traps”, and are most often the result of anthropogenic habitat change (Schlaepfer et al. 2002, Battin 2004).

Anthropogenic habitat changes have caused population declines in numerous species around the world (Kirby et al. 2008). Ecological traps can be caused by extreme habitat changes such as those occurring from agricultural conversion and urbanization, as well as those from subtler changes including the spread of invasive species (Battin 2004). Animals are susceptible to ecological traps when the cues they have evolved to identify quality habitat are no longer accurate (Battin 2004). Specialist species are particularly at risk, and by their nature have less ability to adapt to a changing environment than do generalist species (Clavel et al. 2011). From a species conservation perspective, is it important to elucidate patterns of habitat selection and the adaptive significance of specific habitat features, so that beneficial features can be preserved or restored, while those that create ecological traps or otherwise create negative impacts can be removed or mitigated.

Here, we examine habitat selection at three spatial scales (nest site, nest area, and breeding territory) and its effect on nesting success of a group of ground-nesting, riverine

specialist bird species in Southeast Asia. Sand and gravel (shingle) bars along the Mekong River in northern Cambodia provide breeding habitat for these species, which include River Tern *Sterna aurantia*, River Lapwing *Vanellus duvaucelli*, Great Thick-knee *Esacus recurvirostris*, Small Pratincole *Glareola lactea*, and Little Ringed Plover *Charadrius dubius*. The former three species have experienced population decreases throughout their global ranges (IUCN 2016). In particular, the River Tern is in danger of disappearing from the Mekong region and is considered Critically Endangered in Cambodia (Goes 2013). Population declines of sandbar-nesting birds are thought to be primarily due to low reproductive success rates (Timmins and Men 1998, Claassen et al., in press). The nests of these species are highly vulnerable to predation by avian and mammalian species, flooding due to rainfall and hydropower dam releases, and disturbance from humans and domestic animals (Claassen 2004, Claassen et al., in press). Exploitation in the form of egg harvesting by local people for personal consumption further threatens these species, although egg harvesting has decreased significantly in recent years due to conservation efforts that engage local people in bird nest protection (Sok et al. 2012, Claassen et al., in press). Recent anthropogenic habitat changes that further threaten these species include additional hydropower developments, gold mining, an increase in seasonal small-scale agriculture occurring on sandbars (especially watermelon farming), and the spread of non-native species such as *Mimosa pigra*, an invasive thorny shrub from the tropical Americas.

Permanent site-based conservation for sandbar-nesting birds has been proposed in some areas, although little is known about breeding habitat requirements of these species. The goals of this study were therefore to: 1) identify habitat characteristics that influence

breeding habitat selection of ground-nesting river birds at three spatial scales: nest-site, local, and territory scales, and 2) investigate the effects of habitat selection decisions on reproductive success. This information will aid habitat management and conservation efforts for these regionally threatened species. Furthermore, our results provide insight into habitat selection patterns at multiple spatial scales, and how habitat selection decisions can affect reproductive success.

METHODS

Study area

The study was conducted along an approximately 60-km stretch of the Mekong River between Stung Treng (13°32'N, 105°58'E) and Kratie (12°29'N, 106°14'E) towns in northeastern Cambodia. This stretch of river ranged from 1-11 km wide and comprised approximately 40 permanent islands and hundreds of seasonally-emergent sandbars. Bezuijen et al. (2008) provide a more detailed description of the area. Breeding habitat of focal bird species consisted of sparsely- to moderately-vegetated, seasonally-emergent sand and pebble (shingle) bars, as well as areas of exposed bedrock. In places, native woody shrubs formed dense clusters; native shrub species included *Telectadium edule*, *Homonoia riparia*, *Phyllanthus jullienii*, and *Xantonnea parviflora* (Maxwell et al. 2008). Additionally, the alien invasive thorny shrub *Mimosa pigra* (hereafter, mimosa) grows in dense clusters at the margins of sandbars, as well as scattered across most open sandy areas along with other herbaceous plants, many of which are weedy species that commonly grow in disturbed areas. Sandbars were often used seasonally by local people for livelihood activities such as fishing and farming; watermelons were the primary

agricultural crop grown on sandbars, but in some areas beans or other vegetables were also cultivated. At some breeding sites, fishers and farmers participated in a nest protection program for sandbar-nesting birds (Claassen et al., in press).

Data collection

From 2010-2014, we located and monitored nests of six sandbar-nesting river bird species: River Tern, River Lapwing, Great Thick-knee, Indian Thick-knee, Small Pratincole, and Little Ringed Plover. Nests were monitored every 4.7 ± 3.6 days, on average (90% range: 1-10 days). Eggs were floated to estimate incubation stage (Hays and Lecroy 1971, Westerkov 1950). Nest fates were assessed based on signs at the nest such as direct observations of chicks, adult behavior, eggshell fragments, and predator tracks (Claassen et al., in press). Nests were considered successful if at least one egg hatched, and broods were considered successful if at least one chick fledged. We measured habitat characteristics of each nest as soon as possible after nesting was completed. We measured breeding habitat characteristics at three spatial scales centered on the nest, as well as at a paired random point. Radii of the three spatial scales were 1m (nest site), 10m (nest area), and the average radius of a breeding territory.

Average territory sizes for each species were estimated by randomly selecting ≥ 20 pairs and constructing minimum convex polygons (MCPs) based on field observations conducted throughout the nesting period. MCPs included all areas that were actively defended from predators and competitors, as well as all regularly used foraging areas, but excluded locations that were considered to be occasional forays outside the breeding territory. For species such as River Terns and Small Pratincoles that have overlapping territories with conspecifics, territory area was analogous to breeding season home range.

At each spatial scale, the paired random plots were constrained by the next largest spatial scale of analysis because birds generally select habitat hierarchically with selection at finer scales being determined by selection at coarser scales (Johnson 1980, Jones 2001). For the territory scale, we constrained randomly selected plots to be within an area ten times the radius of the territory. If a random plot was located in an area that was not considered to be available, a new random plot was selected. At the 1-m and 10-m scales a random plot was considered unavailable if it fell in water or in an area with > 50% woody vegetation. At the territory scale, a random plot was considered to be unavailable if it was located in water or upland cover types.

Habitat variables measured are listed in Table 1. At the 1-m and 10-m scales, habitat data were collected directly in the field. Overhead cover and proportions of cover types were visually estimated, and distances and elevation were measured using a laser rangefinder and hypsometer (Nikon Forestry Pro). Habitat characteristics at the territory scale were measured using remote sensing and GIS techniques. First, we conducted an unsupervised classification of satellite imagery of the area (Digital Globe Basemap, WorldView-2, 50cm resolution, pan-sharpened natural color imagery) to create a landcover map with 25 classes (ERDAS Imagine 2013 software). We imported the classified image into ArcMap 10.2.2 and reclassified the landcover map using four classes: bare ground (i.e., areas of sand, dry mud, gravel, and bedrock were combined into a single class), vegetation, water, and upland habitat. We visually inspected the classified image and manually corrected obvious misclassification errors using the ArcMap Raster Edit Suite (ARES version 0.1.3). We intersected used and available plots

with the reclassified landcover raster map to obtain proportions of the different landcover types in each plot (isectpolyrst function, Geospatial Modeling Environment, Beyer 2012).

Statistical analyses

We employed a case-control design to compare used plots to randomly selected unused plots (Manly 2002). Habitat selection was modeled for each species and spatial scale by fitting mixed-effect conditional logistic regressions (package mclogit; R statistical software, version 3.3.0, R Development Core Team 2016). Year and site were modeled as random effects. To avoid problems arising from collinearity (Dormann et al. 2013), habitat variables that were correlated (Pearson correlation, $|r| \geq 0.7$) were not included in the same model. We first modeled each habitat variable separately; if odds ratios had 95% confidence intervals that overlapped 1.0, we did not consider that variable further. To avoid overfitting models, and because some variables were correlated, habitat selection models were constructed using a forward-selection approach, starting with intercept-only models and sequentially adding habitat variables to the best-supported model from the previous step in the model selection process. Models were ranked according to their Akaike's Information Criterion values, adjusted for small sample sizes (AIC_c , Burnham and Anderson 2002). Discriminatory performance of habitat selection models was assessed using the area under the receiver operating characteristic (ROC) curve (AUC); a model with $AUC \geq 0.7$ was considered to have good ability to differentiate between used and control locations (Pearce and Ferrier 2000). Results from habitat selection models were interpreted based on odds ratios such that a one-unit change in a habitat variable (x_1) indicated an $\exp(\beta_1)$ change in the odds ratio (Keating and Cherry 2004).

We evaluated whether habitat characteristics that were included in best-supported models of habitat selection improved daily nest survival rates. For River Terns, we also investigated the effects of habitat characteristics on chick survival. We employed two stages of model development. In Stage 1, we sequentially added habitat variables from the best-supported models of habitat selection to previously described base models of nest and chick survival (Claassen et al., in press); base models included effects of nest age, date, year, and nest protection. In Stage 2, we tested additional habitat covariates beyond those included in the best-supported models of habitat selection. Because vegetation increased during the breeding season, we also tested an interaction effect of vegetation covariates and date. To avoid problems associated with multicollinearity (Battin and Lawler 2006), we did not include habitat variables that were correlated across spatial scales ($|r| \geq 0.7$) in the same model of nest or chick survival. Nest and chick survival were modeled using SAS software (Rotella et al. 2004; NLMIXED procedure, SAS version 9.4, SAS Institute Inc., Cary, NC). We ranked models of nest and chick survival according to their AIC_c values (Burnham and Anderson 2002). We converted nest and chick survival rates to nest and fledging success (likelihood of survival for the entire egg period until hatching and chick period until fledging) to simplify interpretation; for these calculations, we used a 24-day nesting and 22-day fledging period for River Terns, and 31-, 20-, and 26-day nesting periods for River Lapwings, Small Pratincoles, and Little Ringed Plovers, respectively (Claassen et al., in press). We report 85% confidence intervals, because assessing parameters using 85% confidence intervals is consistent with AIC model selection methods (Arnold 2010). Means are reported ± 1 standard deviation (SD), unless otherwise noted.

RESULTS

From 2010-2015, we measured habitat characteristics at 776 nests (River Tern: $n = 79$; River Lapwing: $n = 94$; Great Thick-knee: $n = 16$; Indian Thick-knee: $n = 2$; Small Pratincole; $n = 500$; Little Ringed Plover: $n = 85$). Mean values of habitat variables for each species and spatial scale are reported in Appendix 1. Habitat characteristics at used sites differed from those at control sites for all species and at all spatial scales.

River Tern

The average territory size for River Terns was 121.9 ± 77.9 ha ($n = 24$). Habitat selection models had the best discriminatory performance at the territory scale, followed by the nest-area (10m-radius) scale, and the nest-site (1m-radius) scale (Table 2). The best-supported model of territory-scale selection included a single linear covariate for proportion of bare ground (Table 2). River Terns selected territories that had a higher proportion of bare ground than unused control sites; for every 1% increase in the amount of bare ground, the odds of territory selection by River Terns increased by 42% (Table 3; Figure 1A). The next best territory-scale model, which contained maximum patch size, had 42% of the AIC model weight (w_i), making it nearly as competitive as the best model containing proportion of bare ground (Table 2); however, proportion of bare ground and maximum patch size were components of the same ecological process and were highly correlated ($r = 0.91$). The best-supported habitat selection model at the nest-area scale (10-m radius buffer around the nest) included distance to the river channel and proportion of vegetation (Table 2). River Terns selected areas that were farther from the river channel and had less vegetation (woody or herbaceous) than control sites; for every 1-m

increase in distance from the river channel, the odds of selection by River Terns increased by 4%, and for every 1% increase in vegetative cover, the odds of selection by River Terns decreased by 23% (Table 3). Proportion of vegetative cover was also included in the best model of nest-site (1-m buffer around the nest) selection (Table 2); every 1% increase in vegetative cover at the nest-site scale reduced the odds by 11% that a River Tern would select the area as a nest site (Table 3).

The only habitat variable that was selected for by River Terns that also had an influence on nest success was the proportion of vegetative cover at the nest site (Table 4). Although River Terns selected nest sites with less vegetation (Tables 2 and 3), nests with more vegetation within a 1-m radius had higher probabilities of success (Tables 4 and 5, Figure 2A). When we tested additional habitat covariates in Stage 2 of model development, an interaction between proportion of mimosa at the nest area (10-m) scale was supported, as was an effect of distance to the nearest edge (water or edge vegetation; Tables 4 and 5). In this best-supported model, an increase in the amount of mimosa led to lower nest success; however, the effect was more significant later in the nesting season (Figure 2B). Also, nest success improved with distance to the nearest edge (Figure 2C). Habitat characteristics selected for by River Terns did not influence fledging success of their chicks (Table 4). However, vegetation height at the 10-m scale was included in the best Stage 2 chick survival model (Table 4); taller vegetation at the 10-m scale led to lower survival rates of River Tern chicks (Figure 2D).

River Lapwing

The average size of a River Lapwing territory was 2.8 ± 2.4 ha for River Lapwings ($n = 44$). Habitat selection models had the best discriminatory performance at the nest-area

(10m-radius) scale, followed by the territory scale, and the nest-site (1m-radius) scale (Table 2). At the territory scale, the best-supported model of habitat selection included proportion of bare ground (Table 2). River Lapwings selected territories that had a higher proportion of bare ground than unused control sites; for every 1% increase in the amount of bare ground, the odds of selection increased by 4% (Table 3; Figure 1B). Proportion of bare ground was highly correlated with maximum sandbar size in the territory ($r = 0.78$). At the nest-area scale (10-m radius buffer around the nest), River Lapwings selected areas that had higher proportions of dry mud, gravel, and rock, and lower proportions of water and native woody vegetation. A 1% increase in dry mud, gravel, or rock led to a corresponding increase in the odds of selection by River Lapwings of 5%, 18%, or 3% (Table 3). Moreover, a 1% increase in proportion of water or native shrub cover led to a 10% or 4% decrease in the odds of selection, respectively (Table 3). The best-supported model of nest-site selection included percent overhead cover (Table 2); River Lapwings selected nest sites with little overhead cover and every 1% increase in the amount of overhead cover resulted in a 34% decrease in the odds of selection (Table 3).

The only habitat characteristic selected for by River Lapwings that influenced nest success was the proportion of bare ground at the territory scale (Table 4); nests were more successful when they were located in territories with a higher proportion of bare ground (Table 5). When we included additional habitat covariates during Stage 2, the number of woody stems at the 1-m scale and the proportion of upland cover at the territory scale were also significant predictors of River Lapwing nest survival (Table 4); nest survival decreased when the number of woody stems at the nest site or proportion of upland habitat in the territory increased (Table 5).

Small Pratincole

The average territory size for Small Pratincoles was 88.8 ± 35.2 ha ($n = 24$). Habitat selection models had the best discriminatory performance at the territory scale, followed by the nest-site (1m-radius) and the nest-area (10m-radius) scales (Table 2). Proportion of bare ground was included in the best-supported model of territory-scale selection by Small Pratincoles (Table 2). Pratincoles selected territories that had a higher proportion of bare ground than unused control sites; for every 1% increase in the amount of bare ground, the odds of selection increased by 73% (Table 3; Figure 1C). Proportion of bare ground was highly correlated with maximum sandbar size in the territory ($r = 0.92$). The best-supported model of nest-area (10-m radius buffer around nest) selection by Small Pratincoles included 6 covariates: proportion of gravel, patch size, proportion of water, proportion of rock, distance to nearest vegetative edge, and proportion of crop (e.g., watermelons, beans; Table 2). Compared to unused control sites, Small Pratincoles selected nest areas that were located within larger sandbar patches and that were farther from edge vegetation than control sites (Table 3). Also, Small Pratincoles selected areas that had lower proportions of water and rock; for every 1% increase in the proportion of water or rock, the odds of selection decreased by 5% or 0.5% (Table 3). However, pratincoles selected for gravel and crop cover (watermelons or beans); for every 1% increase in the proportion of gravel or crop cover, the odds of selection increased by 4% or 11%, respectively. At the nest-site scale, Small Pratincoles selected sites with more overhead cover, gravel, debris (wood, bamboo, domestic water buffalo dung, or trash such as glass bottles and plastic objects), and mimosa than unused control sites; for every

1% increase in the values of these habitat variables, the odds of nest-site selection by pratincoles increased by 10%, 10%, 84%, and 17%, respectively (Table 3).

Of the habitat characteristics that were selected for by Small Pratincoles, only proportion of gravel at the nest-area (10-m radius) scale influenced nest success (Table 4); a pratincole nest was more likely be successful if it was located in an area that had a higher proportion of gravel (Table 5). Although proportion of gravel was highly correlated at the nest area (10-m buffer) and nest site scales (1-m buffer; $r = 0.92$), the nest-site scale covariate did not improve nest survival models as much as the nest area covariate; therefore, to avoid issues of cross-scale correlation (Battin and Lawler 2006), we did not consider the nest-site scale covariate for proportion of gravel further. When we included additional habitat covariates in Stage 2 of nest survival model development, distance to river channel and proportions of herbaceous vegetation and damp sand at the nest-area scale were also significant predictors of Small Pratincole nest success (Table 4). The likelihood of successful hatching decreased for nests that were located nearer to the river channel and for nests that had more herbaceous vegetation or damp sand within a 10-m radius (Table 5). Contrary to expectation, correlation between distance to river channel and proportion of damp sand was low ($r = 0.10$), so these two variables were allowed in the same model.

Little Ringed Plover

For Little Ringed Plovers, average territory size was 1.12 ± 1.10 ha ($n = 27$). Habitat selection models had the best discriminatory performance at the nest-area (10m-radius) scale, followed by the nest-site (1m-radius) and territory scales (Table 2). The best-supported model of Little Ringed Plover territory selection included proportion of woody

vegetation and proportion of bare ground (Table 2). Plovers selected territories with a lower proportion of woody vegetation and higher proportion of bare ground than control sites; for every 1% increase in woody vegetation, the odds of selection decreased by 5%, and for every 1% increase in the proportion of bare ground the odds of selection increased by 2% (Table 3). Little Ringed Plovers selected nest areas (10-m radius buffer around nest) with higher proportions of gravel and mimosa than unused control sites; every 1% increase in gravel or mimosa increased the odds of selection by 17% or 31%, respectively (Table 3). The best-supported model of nest-site selection included percent overhead cover and proportion of mimosa. Plovers selected nest sites (1-m radius around nests) with more overhead cover and more mimosa; for every 1% increase in overhead cover or proportion of mimosa, the odds of selection increased by 4% or 9%, respectively (Table 3).

Little Ringed Plover nest success was not influenced by any of the habitat characteristics that were selected for (Table 4). When we added additional habitat covariates during Stage 2 of nest survival model development, distance to the river channel and proportion of herbaceous vegetation at the nest-area scale were significant predictors of Little Ringed Plover nest success (Table 4); the likelihood of successful hatching decreased for nests that were located nearer to the river channel and for nests with more herbaceous vegetation within a 10-m radius (Table 6).

Great and Indian Thick-knee

Average territory sizes were 17.3 ± 12.0 ha for Great Thick-knee ($n = 16$) and 8.5 ± 2.0 ha for Indian Thick-knee ($n = 2$). Due to small sample sizes, we did not model habitat selection or nest success for Great or Indian Thick-knee.

DISCUSSION

Habitat selection was evident for all species and at all spatial scales as habitat characteristics at used locations differed from unused locations. All species selected breeding territories with higher proportions of bare substrates than control sites (Figure 1). However, proportion of bare substrates at the territory scale had the most predictive power for River Terns and Small Pratincoles; accuracy of territory selection models was much lower for River Lapwings and Little Ringed Plovers (Table 2). At smaller spatial scales, selection varied according to species in terms of habitat characteristics selected for, as well as in the predictive power of habitat characteristics at the nest-area and nest-site scales. Despite evidence of breeding habitat selection by the focal species, our results indicated considerable incongruence between habitat characteristics selected for and those that conferred greater fitness in terms of higher reproductive rates. Most variables included in habitat selection models were not accurate predictors of nest success. Other studies have suggested that lack of congruence between habitat selection and breeding success in birds may be due to variation in selective pressures over time, or the existence of ecological traps (Clark and Shutler 1999, Chalfoun and Schmidt 2012).

Nest predation is the primary cause of nest failure among many bird species (Ricklefs 1989, Martin 1993). Ground nests in open habitats are especially at risk of being depredated (Pauliny et al. 2008, Ekanayake et al. 2015). During this study, the primary nest predators were rodents such as Asian House Rat *Rattus tanezumi*, and Southern Jungle Crow *Corvus macrorhynchos* (Claassen et al., in press). Apparent mismatches between habitat selection and reproductive success can occur if predator

communities shift from what birds evolved to contend with (Chalfoun and Shmidt 2012). Specialist species such as riverine ground-nesting birds may not have the behavioral plasticity needed to quickly adapt to rapidly changing conditions (Clavel et al. 2012). Along the Mekong River in northern Cambodia, human population growth and anthropogenic activities such as agricultural and village expansion have increased considerably in recent years (Bezuijen et al. 2008). These changes may have led to increased populations of opportunistic predators such as rats and crows that benefit from human activities (Claassen et al., in press).

In this study, selection by River Terns for nest sites with less vegetation resulted in lower nest success, suggesting a mismatch between habitat selection by River Terns and habitat quality. Tradeoffs between visibility by incubating adults and concealment of nests from predators have been indicated in studies of other systems (Magaña et al. 2010). In this study, we speculate that River Terns chose sites with high visibility for better detection of predators even though sites with some vegetative concealment of the eggs provided better protection from nest predators and improved the chances of successful hatching. Alternatively, River Terns may have been caught in a perceptual trap (Patten and Kelly 2010), whereby they perceived unvegetated areas to be higher quality nesting habitat even though some vegetation at the nest was actually beneficial.

One recent habitat change that may be affecting sandbar-nesting birds' perception of habitat quality is proliferation of the invasive, thorny shrub *M. pigra*, which has become widespread in the Mekong basin since it was introduced in 1947 (Peh 2010). *M. pigra* out-competes native wetland vegetation, and its prevalence in Southern Australia has been related to lower avian diversity and abundance (Braithwaite et al. 1989). In this

study, nest success of River Terns was lower in areas that had more mimosa. Although River Terns did not avoid mimosa per se, they did select nest areas that had less vegetation of any type (mimosa, native shrub, or herbaceous). Along the Mekong River, distribution of mimosa is patchy; in some areas it forms dense thickets, but in other areas it grows sparsely scattered. Both mimosa and native shrubs tended to grow on dunes and other higher areas of sandbars where they grew to be > 1.5m tall. The main factor affecting survival of River Tern nests and chicks was predation by rodents such as Asian House Rat (Claassen et al., in press). Because River Terns tended to select nesting areas with little vegetation, nest success of this species was likely less impacted by mimosa excluding native vegetation than by the fact that mimosa (and other native shrubs) provided cover and burrowing habitat for rodents. Our results indicate that River Tern chick survival was also negatively affected by vegetation in the vicinity of the nest. Chicks were less likely to survive until fledging in areas with taller vegetation. Although chicks required shade and cover, abundance of rodent predators was likely higher in areas with taller woody vegetation. Similar to River Terns, River Lapwings selected areas with less vegetation, and their nests were less successful when the number of woody stems increased.

While River Terns and River Lapwings selected areas with less vegetation, Small Pratincoles and Little Ringed Plovers selected areas with more overhead cover and mimosa. Furthermore, Small Pratincoles selected areas with higher proportions of crops such as watermelon and beans. Presumably, Small Pratincoles and Little Ringed Plovers perceived that nest sites with more shade and concealment from predators were higher quality. However, nest success rates of these species were not affected by overhead

cover, mimosa, or crops. Unlike River Terns that aggressively defend their nests, Small Pratincoles and Little Ringed Plovers employed more passive nest defense behaviors such as distraction displays and cryptic departure from the nest. Perhaps partial concealment of nests by vegetation was effective when combined with aggressive nest defense, but was less effective at preventing detection of nests by visual predators when more passive nest defense strategies were used. Vegetation provided shade, and overheating was likely an issue for eggs, chicks, and incubating adults given the extreme temperatures during the Cambodian dry season (substrate temperatures reached $\geq 50^{\circ}\text{C}$ during the hottest part of the breeding season). However, in this study, belly-soaking behavior by adults was perhaps a more effective means of cooling eggs than choosing shaded nest sites. All focal species except thick-knees were frequently observed belly-soaking. Studies of other waterbird species have found that breeding birds belly soak to cool themselves, eggs, or young (Grant 1982, Amat and Masero 2007). Small Pratincoles and Little Ringed Plovers selected for mimosa, but most mimosa plants near nest sites were relatively small, $< 1\text{-m}$ tall, single-stemmed plants, and did not provide much shade or concealment. On several occasions, we observed Southern Jungle Crows systematically searching and preying on Small Pratincole nests that were located at the bases of mimosa. Also, humans (both community nest protectors and poachers) found nests more readily when they were located at the bases of mimosa. Any benefits, such as shading the eggs, may have been cancelled out by the fact that nesting at the bases of mimosa, which grew scattered across sandbars, provided an efficient search image for intelligent, visual predators such as crows and humans. Crops appeared to provide concealment from crows, and no poachers stole any nests located in crop fields (all crop

fields near monitored nests were owned by community nest protectors). However, crops did not provide protection from mammalian predators, and in fact may have attracted them; in 2012, many nests located in a watermelon field were predated by rodents.

Studies of other ground-nesting waterbirds have documented selection of nest site substrates that provide camouflage against predators (Colwell et al. 2011, Nguyen et al. 2013) or aid in thermoregulation (Saalfeld et al. 2012). In this study, selection for substrate type was evident for Small Pratincoles, Little Ringed Plovers, and River Lapwings, but not for River Terns. The former three species had highly cryptic eggs that blended with their surroundings, but River Tern egg coloration contrasted more markedly with nest substrates. The variation in egg crypsis among species corresponded to their different nest defense strategies. River Terns had the least cryptic eggs, but the most aggressive nest defense. Small Pratincoles and Little Ringed Plovers selected areas with more gravel than random sites. Eggs of these species were especially well camouflaged when located amongst egg-sized gravel. Nesting in gravel improved nest success of Small Pratincoles, but not Little Ringed Plovers. The difference in benefits conferred by gravel substrates for these two species may be due to difference in the primary nest predators; Small Pratincole nest depredations were mainly by Southern Jungle Crows which are visual foragers, whereas Little Ringed Plover nests were primarily predated by rodents which use olfactory cues to locate food (Claassen et al., in press). Also, Small Pratincoles selected nest sites with more debris and objects; although nest site debris has improved nest success of other shorebird species (Hood and Dinsmore 2007), debris at the nest site was not a significant predictor of Small Pratincole nest success in this study. Additionally, River Lapwings selected nest areas that had higher proportions of dry mud

than control sites, but dry mud did not improve nest success. River Lapwing eggs tended to be a similar color to dry mud, but the shapes of the eggs and nest scrape were still discernable, at least to a human observer. River Lapwings frequently partially buried their eggs, sometimes by > 75%, presumably for thermoregulation and concealment (Claassen, pers. obs.). Studies of other ground-nesting waterbird species have also documented egg burying as a means to cool or conceal eggs (Grant 1982, Amat et al. 2012). Although we did not account for this type of egg concealment in our analysis of nest survival, burying eggs almost certainly provided better camouflage from nest predators than cryptic coloration alone.

Habitat selection and nest success of focal species was also influenced by proximity to water. River Terns selected nest areas farther from the river channel and River Lapwings and Small Pratincoles selected nest areas with lower proportions of water than control sites. Small Pratincole and Little Ringed Plover nest success was lower for nests closer to the river channel, and River Tern nest success was lower for nests closer to the nearest edge (water or vegetative). During this study, 4-7% of nest failures of sandbar-nesting birds on the Mekong River were due to inundation (Claassen et al., in press); some of those failures were due to flooding from high rainfall, but others were likely due to water releases from upstream hydropower dams. In a study of the Sesan River, a large tributary of the Mekong River, 37.5% of nest failures of sandbar-nesting birds were due to flooding from an upstream hydropower dam (Claassen 2004). Several additional upstream hydropower dams are currently under construction or have been proposed for the Mekong mainstem and major tributaries such as the Sekong, Sesan, and Srepok (3S) Rivers (Baran and Myschowoda 2009). The location of one of these

proposed dams, the Sambor dam, is just downstream of the study site; if built, this dam will cause inundation of many of the breeding sites that were monitored during this study. In addition to inundating habitat through creation of reservoirs, dams can alter critical breeding habitat for sandbar-nesting birds. Dams trap sediment and, in the Mekong basin, are predicted to cause higher water levels in the dry (breeding) season and lower water levels in the rainy (non-breeding) season (Ligon et al. 1995, Piman et al. 2013). Therefore, fewer new sandbars will be created, fewer areas of existing sandbars will be exposed and available to breeding birds during the dry season, and encroachment of vegetation, especially woody native shrubs and mimosa, will increase without the scouring rainy season flows. Furthermore, hydropower dams negatively impact fish populations (fish are the primary food source of River Terns) by blocking fish migrations (87% of Mekong basin fish are migratory; Ligon et al. 1995, Piman et al. 2013). During this study, nest success rates of sandbar-nesting birds were impacted by water-related habitat factors such as proximity to the river channel, as well as vegetation-related habitat characteristics. Additionally, all sandbar-nesting species selected territories with higher proportions of bare ground (exposed channel substrates), than random control sites. Our results show that sandbar-nesting birds are sensitive to habitat characteristics at multiple spatial scales. These species are adapted to a natural river regime and thus may not be able to easily respond to rapid and extensive habitat changes caused by dams.

Based on our model results, some patterns of habitat selection were clear; for example, proportion of bare ground was a significant and accurate predictor of territory-scale selection by River Terns and Small Pratincoles. However, other habitat features were less accurate predictors of habitat selection. Sample size and species' ecological

characteristics have been shown to influence species distribution models (Hernandez et al. 2006), and likely have similar effects on other types of species models. Small sample sizes of nests in this study likely increased model uncertainty and decreased the predictive ability of models to differentiate used from unused locations. Furthermore, predictive performance of habitat selection models was generally higher for River Terns and Small Pratincoles than for River Lapwings and Little Ringed Plovers (Table 2). This may have been because the former two species have more specialized breeding habitat requirements, whereas broader ecological niches may have reduced the discriminatory ability of habitat selection models for the latter two species. The accuracy of our model predictions should be taken into consideration when making management decisions affecting critical breeding habitat of the focal species.

Despite limitations of this study, it is one of the few habitat selection studies linking selection with reproductive success, and is the first study to document the effects of habitat features on nesting success of the focal species. Although our results indicate considerable incongruence between habitat features that were selected for and those that influenced nest success rates, selection may nonetheless have been adaptive in terms of improving fitness or survival of breeding adults or young. However, assessing fitness or survival of breeding adults or young (other than monitoring River Tern chicks until fledging) was beyond the scope of this study. Despite study limitations, our results provide insights into breeding habitat selection patterns, and the influence of specific habitat features, that will aid conservation efforts for these regionally-threatened species.

Conservation Implications

Habitat protection and other conservation efforts for sandbar-nesting species should prioritize River Tern, because this species is most at risk (Goes 2013, IUCN 2016); next-highest priority should be given to Great Thick-knee and River Lapwing which are also regionally threatened (Goes 2013; IUCN 2016). Results of this study show that sandbar-nesting bird species selected territories with more extensive areas of exposed substrates. Based on these results, conservation efforts should focus on protecting larger sandbars and areas with more extensive areas of exposed substrates. River Tern nest success and chick survival were negatively impacted by woody vegetation such as alien, invasive *Mimosa pigra*. Also, River Lapwing nest success decreased with more woody stems in the nest area. Therefore, removal of encroaching woody vegetation (*Mimosa pigra* and native shrubs) may be warranted at some key breeding sites. Although Small Pratincoles selected sites with more watermelon and other crops, herbaceous vegetation in general had a negative effect on nesting success of both this species and Little Ringed Plover. All sandbar agriculture in the study area was implemented at a small scale by local community members, many of whom participated in a bird conservation program that significantly improved reproductive success of sandbar-nesting birds (Claassen et al., in press). In the future, we recommend that the size of agricultural areas be reduced at key nesting sites to increase the amount of sandbar habitat available to nesting birds; however, we do not recommend completely disallowing sandbar agriculture by nest protectors, because farming provides an important source of supplementary income to nest protectors, without which they might not otherwise have the ability or desire to participate in conservation. Our results suggest that incorporating habitat conservation and management into current nest protection activities could further improve

reproductive success of sandbar-nesting birds in the Mekong River basin. Furthermore, as noted by Claassen et al. (in press), predator control measures such as seasonal removal of rodents should be implemented at key breeding sites. Finally, we recommend that existing hydropower dams be operated under environmental flow regimes that better mimic the natural hydrologic cycle, and that alternative energy sources to hydropower that have fewer negative environmental impacts be explored and developed in the Mekong region.

Table 1. Habitat variable names, descriptions, units of measurement, and scales at which habitat variables were measured.

Variable	Description	Unit	Scale
NumberPatches	Number of patches	count	territory
PatchSize	Maximum patch size	ha	territory
Elevation	Elevation	m	10m
Slope	Slope	%	1m
SoilMoisture	Soil Moisture Index (0=dry, 1=damp, 2=wet)	index	1m
DistWaterAny	Distance to nearest water (any type)	m	10m
DistChannel	Distance to nearest river channel	m	10m
DistHouse	Distance to nearest human habitation	m	10m
DistEdgeVeg	Distance to nearest vegetative edge	m	10m
DistEdgeAny	Distance to nearest edge (vegetative or water)	m	10m
Visibility	Visibility from the nest, averaged for N/E/S/W	m	10m
OverheadCover	Overhead Cover	%	1m
VegHeight	Average vegetation height	m	10m, 1m
WoodyStems	Number of woody stems	count	10m, 1m
PropBareGround	Proportion of bare ground (exposed substrates)	%	territory
PropWoodyVeg	Proportion of woody vegetation	%	territory
PropUpland	Proportion of upland cover	%	territory
PropWater	Proportion of water	%	territory, 10m, 1m
PropDampSand	Proportion of damp or wet sand	%	10m, 1m
PropDrySand	Proportion of dry sand	%	10m, 1m
PropDryMud	Proportion of dry mud	%	10m, 1m
PropGravel	Proportion of gravel (gravel, shingle, or cobble)	%	10m, 1m
PropRock	Proportion of bedrock	%	10m, 1m
PropMimosa	Proportion of <i>Mimosa pigra</i>	%	10m, 1m
PropNativeWoody	Proportion of native woody vegetation	%	10m, 1m
PropWoodyAny	Proportion of woody vegetation (native or mimosa)	%	10m, 1m
PropVegAny	Proportion of vegetation (woody or herbaceous)	%	10m, 1m
PropHerb	Proportion of herbaceous vegetation (non-crop)	%	10m, 1m
PropCrop	Proportion of crop (watermelon or beans)	%	10m, 1m
PropDebris	Proportion of debris	%	10m, 1m

Table 2. Best-supported models of breeding habitat selection of sandbar-nesting birds along the Mekong River, Cambodia, 2010-2014. Next best models and null models are reported for comparison.

Model ^a	ΔAIC_c^b	w_i^c	K^d	Dev ^e	AUC ^f
River Tern					
Territory (598-m radius; $n = 158$)					
PropBareGround	0	0.58	2	51.5	0.85
MaxSandbarArea	0.7	0.42	2	52.1	0.82
PropUpland	41.4	0	2	92.9	0.69
Null	159.2	0	1	213.5	0.50
Nest Area (10-m radius; $n = 158$)					
PropVegAny + DistChannel	0	0.98	3	53.8	0.73
PropVegAny	7.5	0.02	2	63.4	0.72
Null	157.6	0	1	213.5	0.50
Nest Site (1-m radius; $n = 158$)					
PropVegAny	0	1.00	2	103.9	0.59
Null	109.5	0	1	213.5	0.50
River Lapwing					
Territory (88-m radius; $n = 186$)					
PropBareGround	0	0.88	2	112.9	0.66
PropWater	3.9	0.12	2	116.8	0.61
Null	139.2	0	1	252.2	0.50
Nest Area (10-m radius; $n = 186$)					

PropDrymud + PropWater + PropGravel + PropRock + PropNativeWoody	0	0.49	6	89.2	0.70
PropDrymud + PropWater + PropGravel + PropRock	1.3	0.25	5	92.6	0.68
PropDrymud + PropWater + PropGravel + PropNativeWoody	2.0	0.18	5	93.4	0.68
PropDrymud + PropWater + PropGravel	3.7	0.08	4	97.1	0.68
Null	154.5	0	1	252.2	0.50
Nest Site (1-m radius; $n = 184$)					
OverheadCover	0	0.79	2	112.1	0.58
VegHeight	2.6	0.21	2	114.8	0.58
Null	137.2	0	1	249.4	0.50
Small Pratincole					
Territory (521-m radius; $n = 1000$)					
PropBareGround	0	1.00	2	45.6	0.98
MaxSandbarArea	46.9	0	2	92.6	0.97
Null	1330.5	0	1	1378.9	0.50
Nest Area (10-m radius; $n = 920$)					
PropGravel + PatchArea + PropWater + PropRock + DistEdgeVeg + PropCrop	0	0.98	6	485.7	0.64
PropGravel + PatchArea + PropWater + PropRock + DistEdgeVeg	8.1	0.02	5	495.9	0.60
Null	772.3	0	1	1268.1	0.50
Nest Site (1-m radius; $n = 1000$)					
OverheadCover + PropGravel + PropMimosa + PropDebris	0	0.98	5	463.3	0.72
OverheadCover + PropGravel + PropMimosa	7.7	0.02	4	473.0	0.71
Null	909.5	0	1	1378.9	0.50

Little Ringed Plover

Territory (54-m radius; $n = 170$)

PropWoodyVeg + PropBareGround	0	0.88	2	94.9	0.66
PropWoodyVeg	4.0	0.12	2	100.9	0.65
Null	127.6	0	1	230.1	0.50

Nest Area (10-m radius; $n = 170$)

PropGravel + PropMimosa	0	0.99	3	72.9	0.71
PropGravel	8.4	0.01	2	83.5	0.65
Null	155.0	0	1	230.1	0.50

Nest Site (1-m radius; $n = 170$)

OverheadCover + PropMimosa	0	0.85	3	89.0	0.71
OverheadCover	3.5	0.15	2	94.6	0.69
Null	139.0	0	1	230.1	0.50

^a Lowest Akaike's Information Criterion values adjusted for small sample sizes (AIC_c) were: River Tern: 105.9 (Nest Site), 57.9 (Nest Area), 53.5 (Territory); River Lapwing: 114.2 (Nest Site), 107.6 (Nest Area), 99.6 (Territory); Small Pratincole: 471.4 (Nest Site), 497.8 (Nest Area), 47.7 (Territory), and Little Ringed Plover: 93.1 (Nest Site), 77.1 (Nest Area), 98.9 (Territory). + Indicates an additive effect. **Bold** indicates a variable that was also included in the best-supported model of nest survival.

^b The difference in AIC_c value between the model and the best-supported model.

^c Akaike weight.

^d Number of model parameters.

^e Model deviance.

^f Area under the receiver operating characteristic curve.

Table 3. Parameter estimates, standard errors, odds ratios, and 85% confidence intervals of the odds ratios of the best-supported models of habitat selection for each species and spatial scale along the Mekong River, Cambodia, 2010-2014.

Parameter	Estimate	SE	Odds Ratio	85% Confidence Interval	
				Lower	Upper
River Tern					
Territory (598-m radius)					
PropBareGround	0.351	0.095	1.420	1.239	1.628
Nest Area (10-m radius)					
PropVegAny	-0.261	0.075	0.771	0.691	0.859
DistChannel	0.039	0.016	1.040	1.016	1.065
Nest Site (1-m radius)					
PropVegAny	-0.118	0.059	0.889	0.816	0.968
River Lapwing					
Territory (88-m radius)					
PropBareGround	0.034	0.010	1.035	1.020	1.049
Nest Area (10-m radius)					
PropDryMud	0.048	0.018	1.049	1.022	1.077
PropWater	-0.106	0.053	0.899	0.834	0.970
PropGravel	0.165	0.091	1.179	1.035	1.345
PropRock	0.030	0.016	1.031	1.007	1.055
PropNativeWoody	-0.038	0.023	0.963	0.932	0.994
Nest Site (1-m radius)					
OverheadCover	-0.411	0.204	0.663	0.494	0.890
Small Pratincole					
Territory (521-m radius)					
PropBareGround	0.546	0.127	1.727	1.439	2.072
Nest Area (10-m radius)					
PropGravel	0.039	0.007	1.040	1.029	1.051
PatchArea	0.042	0.009	1.043	1.030	1.057
PropWater	-0.054	0.016	0.948	0.926	0.970
DistEdgeVeg	0.502	0.253	1.652	1.147	2.379

PropRock	-0.005	0.002	0.995	0.993	0.998
PropCrop	0.102	0.039	1.108	1.047	1.172
Nest Site (1-m radius)					
OverheadCover	0.093	0.016	1.097	1.073	1.123
PropGravel	0.092	0.020	1.096	1.065	1.129
PropMimosa	0.157	0.039	1.170	1.106	1.237
PropDebris	0.609	0.305	1.838	1.184	2.853
Little Ringed Plover					
Territory (54-m radius)					
PropWoodyVeg	-0.052	0.019	0.949	0.924	0.975
PropBareGround	0.019	0.008	1.019	1.007	1.031
Nest Area (10-m radius)					
PropGravel	0.153	0.063	1.165	1.065	1.276
PropMimosa	0.269	0.115	1.309	1.109	1.544
Nest Site (1-m radius)					
OverheadCover	0.037	0.014	1.038	1.017	1.060
PropMimosa	0.085	0.046	1.088	1.018	1.164

^a Bold indicates a variable that was also included in the best-supported model of habitat selection.

Table 4. Model selection results of nest survival of sandbar-nesting birds along the Mekong River, Cambodia, 2010-2014. All competitive models, the next best model in each candidate set, and the base model are reported.

Model ^a	ΔAIC_c^b	w_i^c	K^d	Dev ^e
River Tern				
Nest Survival ($n = 128$)				
Base + PropVegAny1 + PropMimosa10 \times Date + DistEdgeAny10	0	0.24	7	284.9
Base + PropVegAny1 + PropMimosa10 \times Date + DistEdgeVeg10	0.5	0.19	7	285.4
Base + PropVegAny1 + PropMimosa10 \times Date + PatchArea10	0.6	0.18	7	285.5
Base + PropVegAny1 + PropMimosa10 \times Date + SoilMoisture1	0.6	0.18	7	285.5
Base + PropVegAny1 + PropMimosa10 \times Date	1.3	0.13	6	288.4
Base + PropVegAny1 + PropMimosa10	2.4	0.07	4	293.9
Base	10.7	0.00	2	306.4
Chick Survival ($n = 53$)				
Base + VegHeight10	0	0.87	3	75.5
Base	3.9	0.13	2	81.6
River Lapwing (Nest Survival; $n = 120$)				
Base + PropBareGroundT + WoodyStems1 + PropUplandT	0	0.45	5	201.0
Base + PropBareGroundT + WoodyStems1	1.3	0.23	4	204.5
Base + PropBareGroundT + PropUplandT	1.8	0.18	4	205.0
Base + PropBareGroundT	2.6	0.12	3	207.9
Base	6.1	0.02	2	213.5

Small Pratincole (Nest Survival; $n = 610$)

Base + PropGravel10 + PropHerb10 + PropDamp10 + DistChannel10	0	0.44	9	945.2
Base + PropGravel10 + PropHerb10 + PropDamp10	0.6	0.32	8	947.9
Base + PropGravel10 + PropHerb10 + PropDamp1	1.4	0.21	8	948.7
Base + PropGravel10 + PropHerb10 + DistChannel10	4.9	0.04	8	952.2
Base	14.1	0.00	5	967.5

Little Ringed Plover (Nest Survival; $n = 170$)

Base + PropHerb10 + DistChannel10	0	0.27	4	187.5
Base + PropHerb10 + WoodyStems10	0.4	0.22	4	187.9
Base + PropHerb10	0.6	0.20	3	190.2
Base + DistChannel10	0.7	0.19	3	190.3
Base	1.7	0.12	2	193.4

^a Lowest Akaike's Information Criterion values adjusted for small sample sizes (AIC_c) were: River Tern: 299.8 (nest survival), 84.0 (chick survival); River Lapwing: 211.5; Small Pratincole: 963.5; Little Ringed Plover: 195.8. + Indicates an additive effect. × indicates an interaction. Bold indicates species a variable that was also included in the best-supported model of habitat selection. Base models were: River Tern: NestProtection (nest survival), NestProtection + HatchDate (chick survival), River Lapwing: Year, Small Pratincole: NestAge + Year + InitiationDate + NestProtection, Small Pratincole: InitiationDate (Claassen et al., in press).

^b The difference in AIC_c value between the model and the best-supported model.

^c Akaike weight.

^d Number of model parameters.

^e Model deviance.

Table 5. Parameter estimates, standard errors, and 85% confidence intervals of habitat variables included in the best-supported nest survival models of sandbar-nesting birds along the Mekong River, Cambodia, 2010-2014.

Parameter ^a	Estimate	SE	85% Confidence Interval	
			Lower	Upper
River Tern				
Nest survival				
PropVegAny1	0.1379	0.0640	0.046	0.230
PropMimosa10	0.3459	0.3321	-0.132	0.824
Date	0.0042	0.0064	-0.005	0.013
PropMimosa10 × Date	-0.0088	0.0039	-0.014	-0.003
DistEdgeAny10	0.0181	0.0109	0.002	0.034
Chick survival				
VegHeight10	-1.8150	0.7214	-2.854	-0.776
River Lapwing				
PropBareGroundT	0.0165	0.0076	0.006	0.027
WoodyStems1	-0.1004	0.0458	-0.166	-0.035
PropUplandT	-0.0274	0.0134	-0.047	-0.008
Small Pratincole				
PropGravel10	0.0037	0.0025	0.0001	0.0073
PropHerb10	-0.0224	0.0083	-0.034	-0.011
PropDamp10	-0.0086	0.0031	-0.013	-0.004
DistChannel10	0.0041	0.0025	0.0005	0.0077
Little Ringed Plover				
PropHerb10	-0.0553	0.0322	-0.102	-0.009
DistChannel10	0.0052	0.0035	0.0001	0.0102

^a Bold indicates a variable that was also included in the best-supported model of habitat selection.

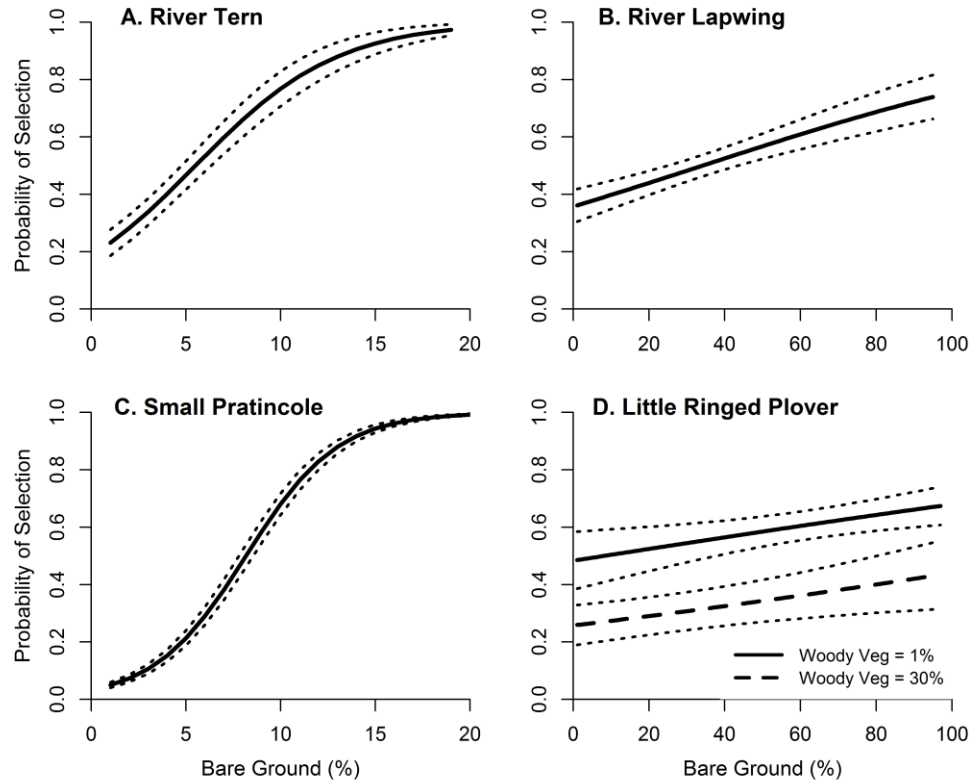


Figure 1. Effect of percent bare ground on model-based probabilities of breeding territory selection by River Terns (A), River Lapwings (B), Small Pratincoles (C), and Little Ringed Plovers (D) along the Mekong River in Cambodia, 2010-2014. Dotted lines indicate 85% confidence intervals.

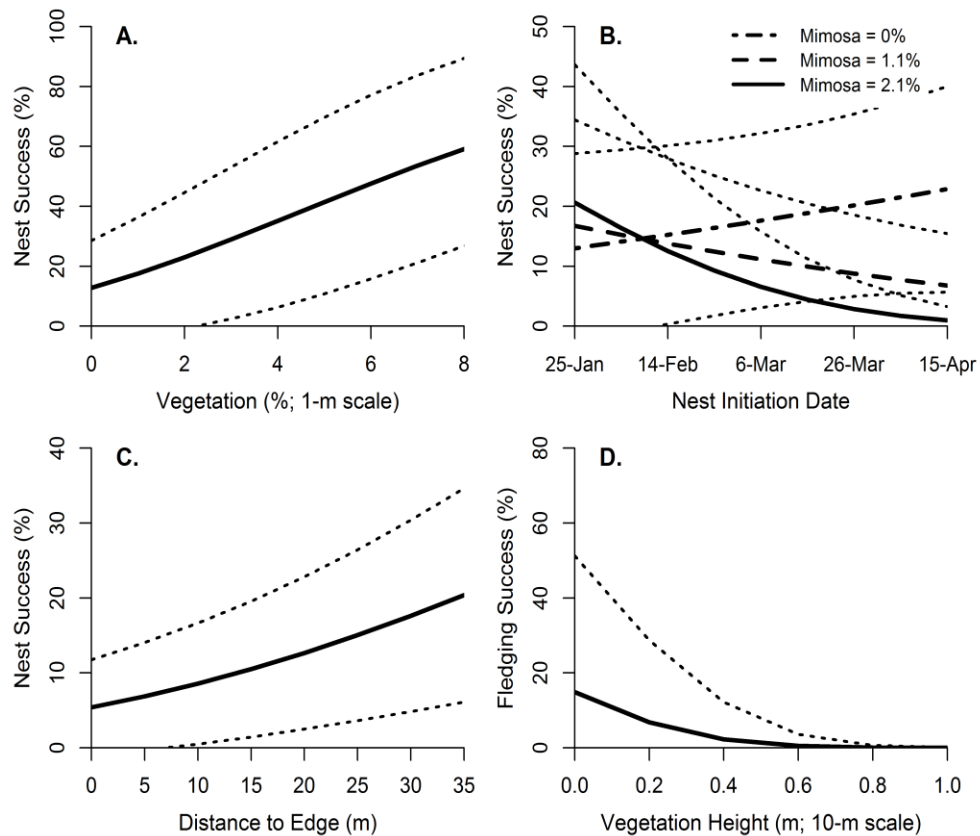


Figure 2. Effects of percent vegetation (1-m scale), interaction between percent mimosa (10-m scale) and nest initiation date, distance to nearest edge on model-based estimates of nest success (A-C), and average vegetation height (10-m scale) on fledging success (D) of River Terns along the Mekong River, Cambodia, 2010-2014. Percent mimosa is shown at 10th percentile (0%), mean (1.1%), and 90th percentile levels (2.1%; B). Covariates for nest and chick protection were held at zero (no protection). Hatch date (fledging success model) was held at the mean value (22 March). Dotted lines indicate 85% prediction intervals.

LITERATURE CITED

- Amat, J. A. and J. A. Masero. 2007. The functions of belly-soaking in Kentish Plovers *Charadrius alexandrinus*. *Ibis* 149(1): 91-97.
- Amat, J. A., R. M. Fraga, and G. M. Arroyo. 1999. Replacement clutches by Kentish Plovers. *Condor* 101:746-751.
- Amat, J. A., R. Monsa, and J. A. Masero. 2012. Dual function of egg-covering in the Kentish plover *Charadrius alexandrinus*. *Behaviour* 149 (8): 881-895.
- Antczak, M., A. Golawski, S. Kuzniak, and P. Tryjanowski. 2009. Costly replacement: how do different stages of nest failure affect clutch replacement in the Red-backed Shrikes *Lanius collurio*? *Ethology, Ecology, and Evolution* 12:127-136.
- Arnold, T. W. 1993. Factors affecting reneesting in American Coots. *Condor* 95:273-281.
- Arnold, T. W. 1999. What limits clutch size in waders? *Journal of Avian Biology* 30:216-220.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175-1178.
- Arnold, J. M., J. J. Hatch, J. J. and I. C. T. Nisbet. 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? *Journal of Avian Biology* 35: 33-45.
- Arnold, T. W., J. H. Devries, and D. W. Howerter. 2010. Factors that affect reneesting in Mallards (*Anas platyrhynchos*). *The Auk* 127:212-221.
- Arnold, T. W., D. W. Howerter, J. H. Devries, B. L. Joynt, R. B. Emery, and M. G. Anderson. 2002. Continuous laying and clutch-size limitation in Mallards. *The Auk* 119: 261-266.
- Baran, E., and C. Myschowoda. 2009. Dams and fisheries in the Mekong Basin. *Aquatic Ecosystem Health and Management* 12(3): 227-234.
- Bates, D. and D. Sarkar. 2006. Lme4: linear mixed-effects modeling using S4 classes. R package, version 2.15.3. [Online]. Available at www.R-project.org.
- Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6): 1482-1491.

- Battin, J., and Lawler, J. J. 2006. Cross-scale correlations and the design and analysis of avian habitat selection studies. *The Condor*, 108(1): 59-70.
- Becker, P. H., and H. Zhang. 2011. Renesting of Common Terns *Sterna hirundo* in the life history perspective. *Journal of Ornithology* 152(Suppl. 1): S213-S225.
- Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.7.3.0). (software). URL: <http://www.spatialecology.com/gme>.
- Bezuijen, M. R., R. Timmins, and Seng T. (eds.). 2008. *Biological surveys of the Mekong River between Kratie and Stung Treng towns, Northeast Cambodia, 2006-2007*. WWF Greater Mekong – Cambodia Country Programme, Cambodia Fisheries Administration, Cambodia Forestry Administration, Phnom Penh, Cambodia.
- Boere, G. C., C. A. Galbraith, and D. A. Stroud. (eds.). 2006. *Waterbirds around the world: A global overview of the conservation, management and research of the world's waterbird flyways*. The Stationery Office, Edinburgh, UK, 960 pp.
- Bonnot, T. W., J. J. Millsaugh, and M. A. Rumble. 2009. Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles. *Forest Ecology and Management* 259(2): 220-228.
- Braithwaite, R. W., W. M. Lonsdale, and J. A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biological Conservation* 48(3): 189.
- Brinkhoff, M. W. G., A. J. Cavé, S. Daan, and A. C. Perdeck. 2002. Timing of current reproductive output in European Coots. *Evolution* 56: 400-411.
- Brudney, L. J., T. W. Arnold, S. P. Saunders, and F. J. Cuthbert. 2013. Survival of Piping Plover (*Charadrius melodus*) chicks in the Great Lakes region. *The Auk* 130: 150-160.
- Burger, J., C. Jeitner, K. Clark, and L. J. Niles. 2004. The effect of human activities on migrant shorebirds: successful adaptive management. *Environmental Conservation* 31: 283-288.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Cairns, W. E. 1982. Biology and behavior of breeding Piping Plovers. *Wilson Bulletin* 94: 531-545.
- Carney, K. M., and W. J. Sydeman. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68-79.

- Chalfoun, A. D., and K. A. Schmidt. 2012. Adaptive breeding-habitat selection: Is it for the birds? *The Auk* 129(4): 589-599.
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behavior* 50: 413-429.
- Claassen, A. H. 2004. *Abundance, distribution, and reproductive success of sandbar nesting birds below the Yali Falls hydropower dam on the Sesan River, Northeastern Cambodia*. WWF, Danida, Wildlife Conservation Society and BirdLife International, Phnom Penh, Cambodia.
- Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 9(4): 222-228.
- Clements, T., A. John, K. Nielsen, An D., Tan S., and E. J. Milner-Gulland. 2010. Payments for biodiversity conservation in the context of weak institutions: comparison of three programs from Cambodia. *Ecological Economics* 69: 1283-1291.
- Clements, T., H. Rainey, An D., Rours V., Tan S., Thong S., W. J. Sutherland, and E. J. Milner-Gulland. 2013. An evaluation of the effectiveness of a direct payment for biodiversity conservation: the bird nest protection program in the Northern Plains of Cambodia. *Biological Conservation* 157: 50-59.
- Colwell, M. A., J. J. Meyer, M. A. Hardy, S. E. Mcallister, A. N. Transou, R. R. Levalley, and S. J. Dinsmore. 2011. Western Snowy Plovers *Charadrius alexandrinus nivosus* select nesting substrates that enhance egg crypsis and improve nest survival. *Ibis* 153(2): 303-311.
- Cornell, K. L., and T. M. Donovan. 2010. Effects of spatial habitat heterogeneity on habitat selection and annual fecundity for a migratory forest songbird. *Landscape Ecology* 25(1): 109-122.
- COSEWIC. 2003. Assessment results. Committee on the status of endangered wildlife in Canada, Ottawa, Canada.
- Cruz, J., R. P. Pech, P. J. Seddon, S. Cleland, D. Nelson, M. D. Sanders, and R. F. Maloney. 2013. Species-specific responses by ground-nesting Charadriiformes to invasive predators and river flows in the braided Tasman River of New Zealand. *Biological Conservation* 167: 363-370.
- Cuthbert, F. J., and E. A. Roche. 2010. Annual report: Piping Plover breeding biology and management in the Great Lakes, 2010. Unpublished Report. Michigan Department of Natural Resources, East Lansing, MI.

- De Neve, L., J. J. Soler, M. Soler, and T. Perez-Contreras. 2004. Differential maternal investment counteracts for late breeding in Magpies *Pica pica*: an experimental study. *Journal of Avian Biology* 35:237-245.
- Devries J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in Mallards (*Anas platyrhynchos*). *The Auk* 125: 618-628.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83(12): 3476-3488
- Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, and T. Münkemüller. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36(1): 27-46.
- Ekanayake, K. B., D. A. Whisson, L. X. L. Tan, and M. A. Weston. 2015. Intense predation of non-colonial, ground-nesting bird eggs by corvid and mammalian predators. *Wildlife Research* 42(6): 518-528.
- Elliott-Smith, E., and S. M. Haig. [online]. 2004. Piping Plover (*Charadrius melodus*). *The birds of North America online*. <http://bna.birds.cornell.edu/bna/species/002/>.
- Ferraro, P. J. (2001) Global habitat protection: limitations of development interventions and a role for conservation performance payments. *Conservation Biology* 15: 990-1000.
- Ferraro, P. J., and H. Gjertsen. 2009. A global review of incentive payments for sea turtle conservation. *Chelonian Conservation and Biology* 8: 48-56.
- Fondell, T. F., J. B. Grand, D. A. Miller, and R. M. Anthony. 2006. Renesting by Dusky Canada Geese on the Copper River Delta, Alaska. *Journal of Wildlife Management* 70: 955-964.
- Gasparini, J., A. Roulin, V. A. Gill, S. A. Hatch, and T. Boulinier. 2006. Kittiwakes strategically reduce investment in replacement clutches. *Proceedings of the Royal Society B* 273: 1551-1554.
- Gilroy, J. J., G. Q. A. Anderson, J. A. Vickery, P. V. Grice, and W. J. Sutherland. 2011. Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. *Animal Conservation* 14(6): 620-629.
- Gjertsen, H., and E. Niesten. 2010. Incentive-based approached in marine conservation: Applications for sea turtles. *Conservation and Society* 8: 5-14.

- Goes, F. 2013. *The birds of Cambodia: An annotated checklist*. Centre for Biodiversity Conservation, Fauna and Flora International Cambodia Program, and Royal University of Phnom Penh, Cambodia.
- Goes, F., A. Claassen, and H. Nielsen. 2010. Obituary to the black-bellied tern. *Cambodian Journal of Natural History* 2010: 5-6.
- Grand, J. B., T. F. Fondell, D. A. Miller, and R. M. Anthony. 2006. Nest survival in Dusky Canada Geese (*Branta Canadensis occidentalis*): use of discrete time models. *The Auk* 123: 198-210.
- Grant, G. S. 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithological Monographs* 30: iii-75.
- Grant, T. A., and T. L. Shaffer. 2012. Time-specific patterns of nest survival for ducks and passerines breeding in North Dakota. *The Auk* 129: 319-328.
- Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation in passerine nest survival: new insights into old questions. *The Auk* 122: 661-672.
- Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and renesting by Greater Sage-grouse. *Journal of Wildlife Management* 70: 472-478.
- Grüebler, M.U., and B. Naef-Daenzer. 2010. Fitness consequences of timing of breeding birds: date effects in the course of a reproductive episode. *Journal of Avian Biology* 41: 282-291.
- Haig, S. M., and L. W. Oring. 1988. Mate, site, and territory fidelity in Piping Plovers. *The Auk* 105: 268-277.
- Harris, W. C., D. D. Duncan, R. J. Franken, D. T. McKinnon, and H. A. Dundas. 2005. Reproductive success of Piping Plovers at Big Quill Lake, Saskatchewan. *Wilson Bulletin* 117: 165-171.
- Hays, H., and M. LeCroy. 1971. Field criteria for determining incubation stage in eggs of the Common Tern. *Wilson Bulletin* 83: 425-429.
- Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29(5): 773-785.
- Hipfner, J. M. 2001. Fitness-related consequences of relaying in an Arctic seabird: survival of offspring to recruitment age. *The Auk* 118: 1079-1080.

- Hood, S. L., and S. J. Dinsmore. 2007. The influence of habitat on nest survival of snowy and Wilson's plovers in the lower Laguna Madre region of Texas. *Studies in Avian Biology* 34: 124-135.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187-211.
- IUCN. 2016. *The IUCN Red List of Threatened Species*. Version 2015.4. www.iucnredlist.org. Accessed 3 August 2016.
- Jaksic, M. 2001. Ecological effects of El Nino in terrestrial ecosystems of western South America. *Ecography* 24: 241-250.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61(1): 65-71.
- Johnson, M., and L. W. Oring. 2002. Are nest enclosures an effective tool in plover conservation? *Waterbirds* 25: 184-190.
- Johnson, M., and J. R. Walters. 2008. Effects of mate and site fidelity on nest survival of Western Sandpipers (*Calidris mauri*). *The Auk* 125: 76-86.
- Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *The Auk* 118(2): 557-562.
- Keating, K. A., and Cherry, S. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* 68(4): 774-789.
- Kershner, E. L., J. W. Walk, and R. E. Warner. 2004. Breeding-season decisions, renesting, and annual fecundity of female Eastern Meadowlarks (*Sturnella magna*) in Southeastern Illinois. *The Auk* 121: 796-805.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83(2): 530-544.
- Kirby, J.S., A. J. Stattersfield, S. H. Butchart, M. I. Evans, R. F. Grimmett, V. R. Jones, J. O'Sullivan, G. M. Tucker, and I. Newton. 2008. Key conservation issues for migratory land-and waterbird species on the world's major flyways. *Bird Conservation International* 18(Suppl. 1): S49-S73.
- Klett, A. T., and D. H. Johnson. 1982. Variability in nest survival rates and implications to nesting studies. *The Auk* 99: 77-81.

- Knetter, J. M., R. S. Lutz, J. R. Cary, and R. K. Murphy. 2002. A multi-scale investigation of Piping Plover productivity on Great Plains alkali lakes, 1994-2000. *Wilson Bulletin* 30: 684-694.
- Lescroël, A., G. Ballard, V. Toniolo, K. J. Barton, P. R. Wilson, P. O. B. Lyver, and D. G. Ainley. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology* 91: 2044-2055.
- Liebezeit, J. R., and T. L. George. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. *The Condor* 104(3): 507-517.
- Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. *BioScience* 45(3): 183-192.
- Lishman, C., E. Nol, K. F. Abraham, and L. P. Nguyen. 2010. Behavioral responses to higher predation risk in a Subarctic population of the Semipalmated Plover. *The Condor* 112: 499-506.
- Mabee, T. J. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bulletin* 109: 307-313.
- Madsen, T., and R. Shine. 1999. Rainfall and rats: Climatically-driven dynamics of a tropical rodent population. *Australian Journal of Ecology* 24: 80-89.
- Magaña, M., J. C. Alonso, C. A. Martin, L. M. Bautista, and B. Martin. 2010. Nest-site selection by Great Bustards *Otis tarda* suggests a trade-off between concealment and visibility. *Ibis* 152(1): 77-89.
- Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11: 299-308.
- Martin, T. E. 1993. Nest predation and nest sites. *BioScience* 43(8): 523-532.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79(2): 656-670.
- Martin, K., and S. J. Hannon. 1987. Natal philopatry and recruitment of Willow Ptarmigan in north central and northwestern Canada. *Oecologia* 71: 518-524.
- Massaro, M., M. Stanbury, and J. V. Briskie. 2013. Nest site selection by the endangered black robin increases vulnerability to predation by an invasive bird. *Animal Conservation* 16(4): 404-411.

- Maxwell, J. F., Kou E., Pranee P., M. van de Bult, Sai J. N., and Choeung H. N. 2008. Vegetation and Flora. In Bezuijen, M. R., Timmins, R. and Seng T. (eds.) *Biological surveys of the Mekong River between Kratie and Stung Treng towns, Northeast Cambodia, 2006-2007*. WWF Greater Mekong – Cambodia Country Programme, Cambodia Fisheries Administration, Cambodia Forestry Administration, Phnom Penh, Cambodia.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. *Ecoscience* 16(2): 238-247.
- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81(10): 2892-2901.
- McGowan, C. P., and M. R. Ryan. 2009. A quantitative framework to evaluate incidental take and endangered species population viability. *Biological Conservation* 142: 3128-3136.
- McPherson, R. J., T. W. Arnold, L. M. Armstrong, and C. J. Schwarz. 2003. Estimating the nest-success rate and the number of nests initiated by radiomarked Mallards. *Journal of Wildlife Management* 67: 843-851.
- Melvin, S. M., L. H. MacIvor, and C. R. Griffin. 1992. Predator exclosures: a technique to reduce predation at Piping Plover nests. *Wildlife Society Bulletin* 20: 143-148.
- Milne, S., and E. Niesten. 2009. Direct payments for biodiversity conservation in developing countries: Practical insights for design and implementation. *Oryx* 43: 530-541.
- Murphy, R. K., I. M. Michaud, D. R. Prescott, J. S. Ivan, B. J. Anderson, and M. L. French-Pombier. 2003. Predation on adult piping plovers at predator exclosure cages. *Waterbirds* 26: 150-155.
- Neuman, K. K., G. W. Page, L. E. Stenzel, J. C. Warriner, and J. S. Warriner. 2004. Effect of mammalian predator management on Snowy Plover breeding success. *Waterbirds* 27: 257-263.
- Nguyen, L.P., E. Nol, K. F. Abraham, and C. Lishman, 2013. Directional selection and repeatability in nest-site preferences of Semipalmated Plovers (*Charadrius semipalmatus*). *Canadian Journal of Zoology* 91(9): 646-652.
- Nol, E., M. S. Blanken, and L. Flynn. Sources of variation in clutch size, egg size and clutch completion dates of Semipalmated Plovers in Churchill, Manitoba. *The Condor* 99: 389-396.
- Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137: S29-S49.

- Parnell, J. F., D. G. Ainley, H. Blokpoel, B. Cain, T. W. Custer, J. J. Dusi, S. Kress, J. A. Kushlan, W. E. Southern, L. E. Stenzel, and B. C. Thompson. 1988. Colonial waterbird management in North America. *Colonial Waterbirds* 11(2): 129-169.
- Pauliny, A., M. Larsson, and D. Blomqvist. 2008. Nest predation management: effects on reproductive success in endangered shorebirds. *Journal of Wildlife Management* 72(7): 1579-1583
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological modelling* 133(3): 225-245.
- Peh, K. S. H. 2010. Invasive species in Southeast Asia: the knowledge so far. *Biodiversity and Conservation* 19(4): 1083-1099.
- Piman, T., T. A. Cochrane, M. E. Arias, A. Green, and N. D. Dat. 2013. Assessment of flow changes from hydropower development and operations in sekong, sesan, and Srepok Rivers of the Mekong Basin. *Journal of Water Resources Planning and Management* 139(6): 723-732.
- Powell, A. N., and F. J. Cuthbert. 1993. Augmenting small populations of plovers: an assessment of cross-fostering and captive-rearing. *Conservation Biology* 7: 160-168.
- Powell, A. N., F. J. Cuthbert, L. C. Wemmer, L. C. Doolittle, and S. T. Feirer. 1997. Captive-rearing Piping Plovers: developing techniques to augment wild populations. *Zoo Biology* 16: 461-477.
- R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricklefs, R. E. 1989. Nest predation and the species diversity of birds. *Trends in Ecology and Evolution* 4(6): 184-186.
- Roche, E. A., T. W. Arnold, and F. J. Cuthbert. 2010. Apparent nest abandonment as evidence of breeding-season mortality in Great Lakes Piping Plovers (*Charadrius melodus*). *The Auk* 127: 402-410.
- Roche, E. A., F. J. Cuthbert, and T. W. Arnold. 2008. Relative fitness of wild and captive-reared Piping Plovers: Does egg salvage contribute to recovery of the endangered Great Lakes population? *Biological Conservation* 141: 3079-3088.
- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27: 187-205.

- Saalfeld, S. T., W. C. Conway, D. A. Haukos, and W. P. Johnson. 2012. Snowy Plover nest site selection, spatial patterning, and temperatures in the Southern High Plains of Texas. *Journal of Wildlife Management* 76(8): 1703-1711.
- Sandercock, B. K., D. B. Lank, and F. Cooke. 1999. Seasonal declines in the fecundity of Arctic-breeding sandpipiers: different tactics in two species with an invariant clutch size. *Journal of Avian Biology* 30: 460-468.
- Sanders, M. D., and R. F. Maloney. 2002. Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. *Biological Conservation* 106(2): 225-236.
- Saunders, S. P., E. A. Roche, T. W. Arnold, and F. J. Cuthbert. 2012. Female site familiarity increases fledging success in Piping Plovers (*Charadrius melodus*). *The Auk* 129: 329-337.
- Saunders, S. P., T. W. Arnold, E. A. Roche, and F. J. Cuthbert. 2014. Age-specific survival and recruitment of piping plovers (*Charadrius melodus*) in the Great Lakes region. *Journal of Avian Biology* 45(5): 437-449.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. (2002). Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17(10): 474-480.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37(11): 789-799.
- Sergio, F., P. Pedrini, and L. Marchesi. 2003. Adaptive selection of foraging and nesting habitat by black kites (*Milvus migrans*) and its implications for conservation: a multi-scale approach. *Biological Conservation* 112(3): 351-362.
- Shaffer, T. L., and F. R. Thompson. 2007. Making meaningful estimates of nest survival with model-based methods. *Studies in Avian Biology* 34: 84-95.
- Shochat, E., M. A. Patten, D. W. Morris, D. L. Reinking, D. H. Wolfe, and S. K. Sherrod. 2005. Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos* 111(1): 159-169.
- Smith, P. A., H. G. Gilchrist, and J. N. M. Smith. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. *The Condor* 109: 15-31.
- Smith, K., A. S. Pullin, G. B. Stewart, and W. J. Sutherland. 2011. Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation* 144: 1-10.

- Sodhi, N. S., M. R. C. Posa, T. M. Lee, D. Bickford, L. P. Koh, and B. W. Brook. 2010. The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation* 19(2): 317-328.
- Sok K., A. H. Claassen, H. L. Wright, and G. E. Ryan. 2012. Waterbird nest protection on the Mekong River: a preliminary evaluation, with notes on the recovery and release of white-shouldered ibis *Pseudibis davisoni* chicks. *Cambodian Journal of Natural History* 2012: 29-41.
- Stanley, T. R. 2000. Modeling and estimation of stage-specific daily survival probabilities of nests. *Ecology* 81: 2048-2053.
- Storaas, T., P. Wegge, and L. Kastdalen. 2000. Weight-related renesting in Capercaillie *Tetrao urogallus*. *Wildlife Biology* 6: 299-303.
- Stucker, J. H., F. J. Cuthbert, B. Winn, B. L. Noel, S. B. Maddock, P. R. Leary, J. Cordes, and L. C. Wemmer. 2010. Distribution of non-breeding Great Lakes Piping Plovers (*Charadrius melodus*) along the Atlantic and Gulf of Mexico coastlines: ten years of band sightings. *Waterbirds* 33: 22-32.
- Suarez, F., J. Traba, and J. Herranz. 2005. Body mass changes in female Tawny Pipits *Anthus campestris* during the nesting stage. *Journal of Ornithology* 146: 372-376.
- Sutherland, W.J., J. A. Alves, T. Amano, C. H. Chang, N. C. Davidson, C. M. Finlayson, J. A. Gill, R. E. Gill, P. M. González, T. G. Gunnarsson, and D. Kleijn. 2012. A horizon scanning assessment of current and potential future threats to migratory shorebirds. *Ibis* 154(4): 663-679.
- Sutherland, W. J., I. Newton, and R. Green. 2004. *Bird ecology and conservation: a handbook of techniques*. Oxford University Press.
- Thewlis, R. M., J. W. Duckworth, T. D. Evans, and R. J. Timmins. 1998. The conservation status of birds in Laos: a review of key species. *Bird Conservation International* 8 (Suppl.): 1-159.
- Timmins, R. J. 2006. *An assessment of the biodiversity conservation significance of the Mekong Ramsar site, Stung Treng, Cambodia*. MWBP, Vientiane, Lao PDR.
- Timmins, R. J., and Men S. 1998. *A wildlife survey of the Tonle San and Tonle Srepok River Basins in Northeastern Cambodia*. Fauna & Flora International, Indochina Programme and Wildlife Protection Office, Department of Forestry, Cambodia.
- Tjørve K. M. C., and L. G. Underhill. 2008. Influence of disturbance and predation on breeding success of the African Black Oystercatcher, *Haematopus moquini*, on Robben Island, South Africa. *Waterbirds* 31: 83-96.

- USFWS. 2003. Recovery Plan for the Great Lakes Piping Plover (*Charadrius melodus*). U.S. Fish and Wildlife Service, Ft. Snelling, Minnesota, USA. viii +141 pp.
- Verboven, N., and J. M. Tinbergen. 2002. Nest desertion: a trade-off between current and future reproduction. *Animal Behavior* 63: 951-958.
- Verboven, N., and M. E. Visser. 1998. Seasonal variation in local recruitment of Great Tits: the importance of being early. *Oikos* 81: 511-524.
- Verhulst S., and J. A. Nilsson. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B-Biological Sciences* 363: 399-410.
- Walk, J. W., K. Wentworth, E. L. Kershner, E. K. Bollinger, and R. E. Warner. 2004. Renesting decisions and annual fecundity of female Dickcissels (*Spiza americana*) in Illinois. *The Auk* 121: 1250-1261.
- Wemmer, L. C., U. Ozesmi, and F. J. Cuthbert. 2001. A habitat-based population model for the Great Lakes population of the Piping Plover (*Charadrius melodus*). *Biological Conservation* 99: 169-181.
- Wendeln, H., P. H. Becker, and J. González-Solis. 2000. Parental care of replacement clutches in Common Terns (*Sterna hirundo*). *Behavioral Ecology and Sociobiology* 47: 382-392.
- Westerkov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14: 56-67.
- Wetlands International. 2012. *Waterbird Population Estimates, Fifth Edition*. Summary Report. Wetlands International, Wageningen, The Netherlands.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional ecology* 3(4): 385-397.
- Winkler, D. W., and J. R. Walters. 1983. The determination of clutch size in precocial birds. *Current Ornithology* 1: 33-6.
- Wright, H. L., N. J. Collar, I. R. Lake, Net N., Rours V., Sok K., Sum P. and P. M. Dolman. 2013. Experimental test of a conservation intervention for a highly threatened waterbird. *Journal of Wildlife Management* 77: 1610-1617.
- Yasué, M., and P. Dearden. 2006. The effects of heat stress, predation risk and parental investment on Malaysian plover nest return times following a human disturbance. *Biological Conservation* 132: 472-480.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York.

Appendix 1: Additional Table for Chapter 3

Table A1. Mean values (\pm SD) of habitat variables measured at nest (used) and control (unused) sites for sandbar-nesting birds on the Mekong River, Cambodia, 2010-2014.

Variable	River Tern		River Lapwing	
	Nest	Control	Nest	Control
Territory	<i>n</i> = 79	<i>n</i> = 79	<i>n</i> = 94	<i>n</i> = 94
bare ground (%)	10.5 \pm 7.6	2.8 \pm 2.9	40.1 \pm 26.3	28.9 \pm 25.0
woody veg (%)	5.5 \pm 4.6	3.5 \pm 5.1	15.3 \pm 8.6	13.7 \pm 10.8
water (%)	62.3 \pm 14.4	61.2 \pm 19.3	40.8 \pm 26.7	50.4 \pm 22.3
upland (%)	21.8 \pm 9.9	32.6 \pm 19.5	3.8 \pm 9.2	7.0 \pm 15.1
# patches	9.5 \pm 9.1	9.0 \pm 16.1	2.1 \pm 1.4	2.5 \pm 1.8
max patch size (ha)	18.4 \pm 17.8	2.4 \pm 3.4	12.6 \pm 16.6	10.6 \pm 16.4
Nest Area	<i>n</i> = 79	<i>n</i> = 79	<i>n</i> = 94	<i>n</i> = 94
elevation (m)	0.95 \pm 0.64	1.04 \pm 1.00	1.09 \pm 0.62	0.94 \pm 0.70
distance water (any; m)	38.5 \pm 42.6	33.5 \pm 40.8	30.8 \pm 30.5	30.1 \pm 36.4
distance channel (m)	86.6 \pm 104.7	75.0 \pm 106.7	99.8 \pm 169.0	94.8 \pm 168.5
distance house (m)	542.2 \pm 474.2	539.5 \pm 477.2	528.4 \pm 406.7	523.9 \pm 408.5
veg height (cm)	43.5 \pm 39.9	79.2 \pm 63.7	86.4 \pm 59.5	90.2 \pm 63.7
# woody stems	42.0 \pm 82.0	88.9 \pm 132.3	128.8 \pm 181.5	135.3 \pm 178.0
distance edge veg (m)	34.9 \pm 80.8	32.0 \pm 82.5	13.8 \pm 14.9	14.0 \pm 16.6
patch area (ha)	43.0 \pm 75.7	45.7 \pm 82.9	40.5 \pm 102.0	39.6 \pm 102.1
visibility (m)	152.4 \pm 103.0	141.9 \pm 107.9	99.8 \pm 72.3	106.1 \pm 82.1
wet sand (%)	9.0 \pm 19.3	7.1 \pm 13.3	3.7 \pm 8.5	8.1 \pm 15.7
dry sand (%)	62.4 \pm 36.6	52.3 \pm 33.6	40.2 \pm 30.9	42.0 \pm 34.4
dry mud (%)	5.8 \pm 14.1	5.5 \pm 14.2	19.4 \pm 24.6	10.5 \pm 19.2
gravel (%)	3.3 \pm 11.9	2.3 \pm 9.3	4.4 \pm 11.4	3.5 \pm 10.1
rock (%)	6.6 \pm 19.1	6.3 \pm 18.1	12.7 \pm 23.2	9.6 \pm 19.8
water (%)	5.8 \pm 14.7	7.2 \pm 13.3	2.1 \pm 4.9	5.8 \pm 10.6
mimosa	1.0 \pm 1.5	1.4 \pm 1.9	2.1 \pm 2.8	1.9 \pm 2.4
native shrub (%)	3.2 \pm 5.6	12.3 \pm 16.4	10.3 \pm 10.7	14.0 \pm 16.2
herb (non-crop; %)	2.8 \pm 4.0	4.3 \pm 7.7	4.0 \pm 4.6	3.1 \pm 4.5
crop (%)	0	52.3 \pm 33.14	0	0
woody debris (%)	0.04 \pm 0.19	0.06 \pm 0.56	0.11 \pm 0.58	0.04 \pm 0.25
Nest Site	<i>n</i> = 79	<i>n</i> = 79	<i>n</i> = 92	<i>n</i> = 92
slope (%)	3.9 \pm 5.0	5.0 \pm 5.4	8.5 \pm 9.0	10.0 \pm 10.1
soil moisture (index)	1.19 \pm 0.56	1.24 \pm 0.62	1.02 \pm 0.15	1.15 \pm 0.53
overhead cover (%)	0.01 \pm 0.11	1.05 \pm 4.69	0.75 \pm 6.27	3.37 \pm 11.36
veg height (cm)	4.8 \pm 13.2	14.7 \pm 58.5	10.4 \pm 15.0	22.0 \pm 33.9
# woody stems	0.19 \pm 0.74	0.42 \pm 1.34	1.5 \pm 3.4	2.0 \pm 4.8
wet sand (%)	15.3 \pm 34.3	16.1 \pm 34.5	0.98 \pm 7.38	5.7 \pm 19.0
dry sand (%)	65.4 \pm 42.9	66.3 \pm 42.0	45.4 \pm 38.2	48.7 \pm 39.7
dry mud (%)	4.4 \pm 14.9	3.2 \pm 13.1	25.6 \pm 35.5	19.3 \pm 31.0
gravel (%)	4.4 \pm 17.0	2.9 \pm 10.6	7.6 \pm 22.3	5.6 \pm 19.4
rock (%)	8.5 \pm 25.1	8.0 \pm 23.6	13.8 \pm 27.1	11.7 \pm 24.8
mimosa (%)	0.34 \pm 1.46	0.82 \pm 2.89	0.49 \pm 1.35	0.62 \pm 2.45
native shrub (%)	0.13 \pm 1.13	0.52 \pm 2.73	1.9 \pm 4.8	4.3 \pm 10.2
herb (non-crop; %)	1.4 \pm 3.0	1.9 \pm 3.7	3.6 \pm 5.1	3.7 \pm 6.2
crop (%)	0	0	0	0
woody debris (%)	0.13 \pm 1.13	0.14 \pm 0.80	0.76 \pm 2.74	0.22 \pm 1.89

Table A1. Continued.

Variable	Small Pratincole		Little Ringed Plover	
	Nest	Control	Nest	Control
Territory	<i>n</i> = 500	<i>n</i> = 500	<i>n</i> = 85	<i>n</i> = 85
bare ground (%)	17.5 ± 5.0	1.3 ± 2.7	56.4 ± 30.2	44.5 ± 29.4
woody veg (%)	1.10 ± 1.90	1.39 ± 1.39	8.3 ± 10.5	14.4 ± 13.7
water (%)	68.8 ± 7.0	83.5 ± 15.0	35.3 ± 27.1	40.8 ± 28.2
upland (%)	12.6 ± 6.9	13.8 ± 15.0	0	0.29 ± 1.47
# patches	3.4 ± 2.2	1.8 ± 2.3	1.4 ± 0.8	1.5 ± 0.9
max patch size (ha)	34.0 ± 12.0	2.3 ± 5.2	23.6 ± 18.2	22.9 ± 18.2
Nest Area	<i>n</i> = 460	<i>n</i> = 460	<i>n</i> = 85	<i>n</i> = 85
elevation (m)	0.85 ± 0.55	0.83 ± 0.51	0.94 ± 0.73	0.90 ± 0.69
distance water (any; m)	37.1 ± 29.8	35.1 ± 26.3	29.83 ± 29.78	26.6 ± 28.1
distance channel (m)	39.8 ± 30.8	37.6 ± 27.6	61.7 ± 83.3	57.7 ± 87.2
distance house (m)	335.4 ± 158.2	333.3 ± 149.1	367.6 ± 360.1	371.2 ± 358.7
veg height (cm)	30.9 ± 29.0	31.9 ± 25.7	76.7 ± 45.5	76.8 ± 53.0
# woody stems	14.6 ± 25.2	14.7 ± 22.2	57.7 ± 83.8	42.5 ± 51.2
distance edge veg (m)	183.0 ± 198.2	195.6 ± 211.7	70.9 ± 119	70.4 ± 123.0
patch area (ha)	171.4 ± 96.7	165.4 ± 95.9	84.5 ± 103.6	79.3 ± 104.3
visibility (m)	341.8 ± 79.6	338.6 ± 77.5	162.2 ± 126.5	155.0 ± 123.7
wet sand (%)	8.3 ± 22.0	9.9 ± 21.2	5.0 ± 15.4	8.3 ± 19.0
dry sand (%)	54.6 ± 36.5	60.5 ± 33.3	58.7 ± 31.8	66.4 ± 30.1
dry mud (%)	5.4 ± 18.8	5.6 ± 13.0	2.2 ± 8.2	2.3 ± 6.7
gravel (%)	18.5 ± 29.5	9.4 ± 19.1	16.9 ± 25.7	3.6 ± 12.0
rock (%)	0.87 ± 6.24	0.44 ± 3.60	2.0 ± 10.8	1.5 ± 8.2
water (%)	3.0 ± 8.5	5.2 ± 11.1	1.2 ± 3.7	4.0 ± 10.3
mimosa	2.4 ± 4.6	2.2 ± 1.9	3.86 ± 5.32	2.44 ± 2.35
native shrub (%)	0.37 ± 1.79	0.61 ± 2.40	5.8 ± 9.4	7.6 ± 13.3
herb (non-crop; %)	4.5 ± 7.7	4.5 ± 5.6	3.0 ± 4.6	2.9 ± 4.5
crop (%)	1.6 ± 5.7	1.1 ± 3.7	0.93 ± 4.39	1.00 ± 4.22
woody debris (%)	0.06 ± 0.50	0.004 ± 0.09	0.05 ± 0.26	0.01 ± 0.11
Nest Site	<i>n</i> = 500	<i>n</i> = 500	<i>n</i> = 85	<i>n</i> = 85
slope (%)	2.9 ± 4.5	3.8 ± 7.9	2.3 ± 3.8	4.7 ± 13.9
soil moisture (index)	1.11 ± 0.43	1.16 ± 0.52	1.00 ± 0	1.19 ± 0.59
overhead cover (%)	13.8 ± 24.3	3.8 ± 13.2	19.9 ± 30.7	20.5 ± 25.8
veg height (cm)	17.5 ± 22.7	13.7 ± 19.6	34.3 ± 39.7	50.7 ± 48.7
# woody stems	0.56 ± 1.21	0.70 ± 3.96	1.4 ± 2.2	3.9 ± 8.4
wet sand (%)	6.3 ± 22.3	7.7 ± 24.1	0.12 ± 1.08	8.74 ± 24.76
dry sand (%)	51.4 ± 37.0	56.5 ± 40.0	59.3 ± 35.6	45.4 ± 36.8
dry mud (%)	4.4 ± 17.2	5.8 ± 20.2	0.24 ± 2.17	4.8 ± 17.7
gravel (%)	25.0 ± 36.0	20.2 ± 32.6	20.9 ± 35.3	21.0 ± 32.8
rock (%)	1.7 ± 12.1	1.4 ± 10.4	4.2 ± 19.2	0
mimosa (%)	3.7 ± 7.7	1.7 ± 4.9	6.1 ± 12.7	9.5 ± 16.0
native shrub (%)	0.01 ± 0.23	0.09 ± 0.92	5.1 ± 12.1	4.3 ± 12.0
herb (non-crop; %)	4.9 ± 8.9	4.5 ± 9.0	3.8 ± 13.7	4.8 ± 8.1
crop (%)	1.8 ± 6.5	1.3 ± 5.1	0	1.2 ± 4.9
woody debris (%)	0.17 ± 1.05	0.07 ± 0.67	0.20 ± 1.07	0.07 ± 0.65

Table A1. Continued.

Variable	Great Thick-knee	Indian Thick-knee
	Nest	Nest
Territory	<i>n</i> = 16	<i>n</i> = 2
bare ground (%)	40.0 ± 20.2	53.1 ± 1.3
woody veg (%)	11.8 ± 4.8	16.7 ± 2.8
water (%)	45.7 ± 19.0	30.2 ± 4.1
upland (%)	2.5 ± 4.9	0
# patches	3.3 ± 3.2	1.0 ± 0
max patch size (ha)	28.7 ± 17.1	24.6 ± 20.1
Nest Area	<i>n</i> = 16	<i>n</i> = 2
elevation (m)	0.90 ± 0.56	1.70 ± 0.42
distance water (any; m)	52.8 ± 53.9	52.5 ± 26.2
distance channel (m)	69.2 ± 55.3	52.5 ± 26.2
distance house (m)	462.4 ± 308.3	643.5 ± 504.2
veg height (cm)	117.5 ± 64.1	100.0 ± 56.6
# woody stems	118.0 ± 77.1	127.5 ± 102.5
distance edge veg (m)	10.3 ± 15.8	7.0 ± 1.4
patch area (ha)	27.6 ± 64.0	3.7 ± 1.8
visibility (m)	63.7 ± 72.6	36.3 ± 14.1
wet sand (%)	6.9 ± 11.5	7.5 ± 10.6
dry sand (%)	28.1 ± 24.9	14.5 ± 7.8
dry mud (%)	33.5 ± 31.6	61.5 ± 9.2
gravel (%)	2.3 ± 4.7	0
rock (%)	4.5 ± 15.2	0
water (%)	0.73 ± 1.94	0
mimosa	1.13 ± 2.33	1.00 ± 0
native shrub (%)	18.7 ± 13.8	11.0 ± 1.4
herb (non-crop; %)	3.0 ± 4.5	4.5 ± 5.0
crop (%)	0	0
woody debris (%)	0	0
Nest Site	<i>n</i> = 16	<i>n</i> = 2
slope (%)	5.5 ± 2.9	8.5 ± 9.2
soil moisture (index)	1.00 ± 0	1.00 ± 0
overhead cover (%)	11.6 ± 20.2	0
veg height (cm)	60.5 ± 58.6	65.0 ± 77.8
# woody stems	4.9 ± 6.8	4.0 ± 5.7
wet sand (%)	0.33 ± 1.29	0
dry sand (%)	29.5 ± 28.4	7.5 ± 3.5
dry mud (%)	42.4 ± 43.0	76.5 ± 9.2
gravel (%)	8.5 ± 17.8	0
rock (%)	3.2 ± 11.1	0
mimosa (%)	0.27 ± 0.80	0
native shrub (%)	13.6 ± 15.0	10.0 ± 14.1
herb (non-crop; %)	2.3 ± 3.7	6.0 ± 8.5
crop (%)	0	0
woody debris (%)	0	0