EXAMINING PATTERNS IN NEST PREDATION USING ARTIFICIAL NESTS

by

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The use of artificial nests to study the predation of avian nests has faced disregard by ecologists due to inconsistencies found between the survival rates of real and artificial nests across studies and reviews. The negative perception of artificial nests providing an inconsistent assessment of survival has thus fostered the perception that artificial nests are a secondary option to be used to overcome logistical hurdles associated with achieving sufficient sample sizes in systems where study species are rare or elusive, or as merely a preliminary method to study predation across gradients. We argue that the greatest mistake ecologists have made with artificial nests is not the flaws within poorly designed studies, but rather the failure to look for patterns in inconsistencies between properly designed studies. Therefore, we conducted a case study to demonstrated the utility of artificial nests as a tool to consistently measure inherent nest predation risk across a set of manipulated experimental treatments. We also conducted a meta-analysis to examine the patterns of real and artificial nest survival across several gradients theorized to influence nest survival (e.g., absolute latitude). We used only data from peer-reviewed journal articles where researchers recorded the survival of both real and artificial nests, to demonstrate that when extraneous variation is reduced inconsistencies give way to prominent patterns in survival.

DEDICATION

To Mom and Dad, for your unconditional love and encouragement;

to Grandma, for your guidance and enthusiasm;

and to Quintin, for being there every step of the way.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: EVALUATING THE UTILITY OF ARTIFICIAL NESTS: A META-ANALYSIS

ABSTRACT

Although the use of artificial nests is alluring due to the ability to overcome logistical hurdles associated with achieving sufficient sample sizes and ease of conducting controlled experiments, many ecologists disparage artificial nest studies because of inconsistencies between the survival rates of real and artificial nests. Further investigation into patterns in inconsistencies between properly designed studies is required to determine the utility of artificial nests. Thus, we conducted a meta-analysis to examine how broad ecological patterns from theory and methodology influenced the difference between real and artificial nest survival. While individual studies may exhibit some variation, the diversity in species (n = 128), habitats (n = 5), and locations (34 countries from 7 continents) of the 245 studies (from 138 peer-reviewed journal articles) we incorporated into our meta-analysis create strong support for the predicted pattern of slightly lower survival for artificial nests than real nests. In addition, the consistency with which the artificial nest survival patterns matched the survival patterns of the real nests indicated that artificial nests are useful tools that can improve our understanding of avian systems when careful consideration of assumptions is practiced. However, the approach used to analyze nest survival appears to influence the patterns of nest survival observed. Thus, when comparing the survival of artificial and real nests, researchers should be cautious of comparing survival results using different approaches.

INTRODUCTION

Nest predation is the primary cause of reproductive failure for most avian species and, therefore, a key component of population dynamics (Ricklefs 1969; Thomas E.

Martin 1995). However, understanding causes and patterns of nest predation is often difficult due to the logistical issues associated with locating a sufficient number of nests within treatment groups to perform statistical analyses (Moore and Robinson 2004). In an attempt to overcome the logistical hurdles of nest studies, many researchers use artificial nests (Moore and Robinson 2004). Although the use of artificial nests is alluring due to the ease of manipulating controlled experiments, many ecologists are wary artificial nest studies because of inconsistencies between the survival rates of real and artificial nests (Buler and Hamilton 2000; Zanette 2002; Moore and Robinson 2004).

Some of the inconsistencies between real and artificial nest studies may result from poor study design that fails to result in artificial nests that adequately mimic natural nests (Moore and Robinson 2004; Major and Kendal 1996). Nest appearance influences the likelihood of predators successfully finding nests, suggesting that differences in nest construction and egg color could create unintended differences between patterns of real and artificial nest survival rates (Thomas E. Martin 1987; Solís and de Lope 1995). Similarly, the utility of artificial nests differs by nest predator community (Greene 1997; Thompson and Burhans 2004). In areas where snakes are a predominant nest predator, for example, inaccurate estimations of predation rates may occur because artificial nests lack the scent and heat signatures snakes use to find nests (Greene 1997; Thompson and Burhans 2004). Indeed, the reported causes of why real and artificial nests are ‘different’ abound in the literature (Moore and Robinson 2004; Major and Kendal 1996), leading many researchers to believe that artificial nests do not have utility in understanding patterns of nest predation (Faaborg 2004).

Although comparing real and artificial nest success may be inappropriate in some systems, careful study design and an understanding of the assumptions associated with artificial nests may be the key to unlocking the true utility of artificial nests (Moore and Robinson 2004). We should consider artificial nests as a tool to study how nest predation shapes avian systems rather than actual nest predation (Villard and Part 2004). For example, environmental variation in nest predation risk ostensibly favors different parental care strategies (Lima 2009; J. J. Fontaine and Martin 2006), but how individuals respond to specific environmental conditions also varies (Ghalambor and Martin 2001; Weidinger 2002). Some parents may select habitats where risk is low and in doing so express behaviors that are more risky (J. J. Fontaine and Martin 2006; J. J. Fontaine and Martin 2006), whereas other parents may select habitats that are more risky, but express less risky behaviors. Despite clear differences in the inherent environmental risk between two habitats, the realized nest predation rates might not differ because parents in both environments attempt to optimize the trade-off between the inherent nest predation risk present in the environment and the benefit of expressing risky parental care strategies (Lima 2009; J. J. Fontaine and Martin 2006; J. J. Fontaine and Martin 2006). Artificial nests allow researchers to examine the inherent predation risk associated with a specific environmental factor (e.g., nest distance from edge habitat) by eliminating individual variation in parental care strategies that may confound the true patterns of environmental predation risk (Lima 2009; J. J. Fontaine and Martin 2006).

We aimed to understand how predation patterns vary between real and artificial nests by asking how the consistency of differences in real and artificial nest survival rates varies across different systems. By improving our understanding of variation between natural and model systems, we will be able to determine when proxies (such as artificial nests) are useful and valid in the pursuit of answering questions that are difficult to answer within natural systems. Specifically, we examined whether consistent patterns in predation are present across absolute latitude, exposure period, nest size, nest type, nest placement, and habitat type by conducting a meta-analysis of artificial nest papers.

METHODS

Article Collection

We used Google Scholar (Google, Mountain View, CA) to search for articles that contained the entire phrase “artificial nest” and either the word “avian” or “bird” within the article’s text to return avian specific articles using artificial nests (6,792 search results). We then compiled articles that contained artificial avian nests based on information in the title and abstract, avoiding articles that focused on artificial nest structures created by people for bird use or non-avian study species, and used the citation management program Zotero (Roy Rosenweig Center for History and New Media) to download articles and store citations (1,167).We then sorted articles based on media type (book, journal article, thesis, or report) and the article type (experiment, comment, meta-analysis, not relevant, or review; see Appendix A for full description of each article type) to focus on peer-reviewed articles that possessed experiments with subject matter pertaining to artificial nests. To avoid repetition from theses that were later published and ensure all articles were peer-reviewed, we limited our meta-analysis to journal articles. After we had pooled journal articles that contained an artificial nest experiment, we selected articles suitable for our meta-analysis based on the use of artificial nests and real nests in experiments rather than artificial nests alone (see Appendix A).

Article Assessment

We assessed 191 articles designated as peer-review journal articles with artificial and real nest experiments based on three areas of interest. First, we recorded general information (e.g., publication date, journal, years of study, location of the research, etc., Appendix B) to summarize trends in artificial nest studies over time. Second, we collected data on the methods used (e.g., species studied, nest type, nest placement, type of eggs used, exposure period, etc., Appendix C) to examine variation between articles and subset experiments with similar nest characteristics and system in our meta-analysis. If articles did not include all pertinent nest characteristic information (as was often the case with egg length and egg width), we attempted to fill in missing background system information using the Birds of North America database to find information on nesting characteristics (Rodewald 2015), the “CRC Handbook of Avian Body Masses” to look up adult body mass (Dunning Jr 2007), and “The Book of Eggs” along with other peer-reviewed journal articles to find the egg length and widths (Hauber 2014). Third, we recorded the questions addressed, treatments used, and the survival rates reported for both artificial and real nests (Appendix D). If an article included results from multiple species, nest types, questions, or other variables that were of interest (e.g., types of eggs, habitats, distances from edge habitat, etc.) that were separable, multiple data entries were created to record the survival results associated with each unique “study”. If studies within articles were based on a treatment manipulated by researchers and a control for the experiment (e.g., predator removal and non-predator removal plots), only the results from the control were included in overall meta-analysis to reduce variation based on unnatural conditions. If treatments within studies were separable and not manipulated by researchers, we recorded treatments separately and either analyzed the treatments individually to examine the effects of specific treatments on survival differences between real and artificial nests (e.g., vegetation density: low versus high) or averaged survival across treatments when variables were not of interest (e.g., species of shrub nests were placed in). We used Access to record and store our data in a database organized by unique IDs specifying the treatment associated with a study within an article for each row of data (Microsoft Access 2013, Microsoft Corporation, Redmond, WA).

Meta-Analysis

To meet our requirements for inclusion in the meta-analysis, an article had to include survival results from both artificial and real nests in comparable forms (138 articles). We used separate models to analyze the survival patterns of the two survival metrics separately, to avoid extraneous variation. The two survival metrics we used were apparent nest success (number of nests survived/total number of nests, hereafter ANS, 110) and daily survival rate (predicted probability of a nest surviving a single day, hereafter DSR, 45, Mayfield 1975). We converted daily survival rate to nest survival rate (daily survival rate ^ number of incubation days, hereafter NSR, (Mayfield 1975) to allow comparisons between patterns in the analyses of apparent nest success and nest survival rates.

We began our analyses by first examining the distribution of our survival and methodological data to assess our ability to examine the patterns of real and artificial nest survival across variables previously shown to influence nest survival (e.g., absolute latitude, (McKinnon et al. 2010; Roper, Sullivan, and Ricklefs 2010; Thomas E. Martin 1996)). We then created separate real and artificial nest data sets by selecting the survival rates for each to ensure any repeated results were removed (e.g., if a treatment was only assigned to artificial nests, then the results from the real nests were repeated in each row associated with the study). We then created universal covariates to bring real and artificial nest information into the same covariates (we created an exposure covariate that was incubation days for real nests and exposure days for artificial nests, Appendix E). Once the real and artificial nest data sets possessed the same covariates and a "nest" covariate to indicate if results were from real or artificial nests, we combined the data sets into separate ANS and NSR data sets, allowing us to analyze the survival of real and artificial nests separately within the same model for each survival metric.

We used generalized linear mixed effects models (glmm, Bates et al. 2015) with a binomial logit link to analyze patterns in the survival of real and artificial nests. In each model, we included our unique article ID as a random effect to account for data from the same article being more similar, and specified whether the data was from real or artificial nests using the nest covariate as a fixed effect. We also accounted for variation in predation risk associated with differences in lengths of exposure by incorporating the number of days nests were exposed into each model as a fixed effect. We then began by examining the effects of nest guild against exposure days by incorporating nest type groups (e.g., open cup, closed cup, cavity, etc.) and nest placement (e.g., ground, shrub, canopy) as fixed effects into two glmm models. After examining nest type and placement separately, we subset data to the most common nest type and nest placements to account for variation associated with nest guild and reduce the constraints of small sample sizes, allowing us to drop nest type and only include nest placement as a fixed effect in the remaining models. We then separately examined the fixed effects of absolute latitude, habitat type, nest size (total clutch volume calculated by multiplying egg volume by clutch size), and number of nest visits (average number of times researchers visited the nest) on the patterns of real and artificial nest survival in a series of eight models, ANS and NSR glmm for each covariate of interest. We compared sets of models with additive and interactive fixed effects for our nest type, nest placement, absolute latitude, habitat, nest size, and nest visits models using AIC to determine the relationships between our fixed effects. After selecting our top model, we then created predictive survival plots using the predict function from package ‘lme4’ (Bates et al. 2015).

RESULTS

Data Collection Summary

We downloaded 1,167 out of 6,792 articles returned by our Google Scholar search. In total, we had 912 journal articles, of which 562 were experiments and 191 used both real and artificial nests. Out of 191 articles that used real and artificial nests, 138 reported the survival of both real and artificial nests in the same survival metric. After separating species, nest placement, nest types, experiments, and treatments into individual rows of data, we had a total of 245 studies that resulted in 668 treatments that included both real and artificial nest survival results (426 ANS, 270 NSR, and 50 with both survival metrics). When we separated out the real and artificial nest survival results into individual data sets, averaged treatments that were not of interest, and removed repeated data, we had a data frame of 159 and 171 ANS treatments respectively and 80 and 60 NSR treatments respectively.

Article Background Information Summary

The earliest article in our data base of real and artificial nest articles was from 1976, but articles using artificial nests did not begin to gain popularity until the late 1980s, and the use of both real and artificial nests did not become popular until the late 1990s (Figure 2.1). The majority of the articles had a study length of less than or equal to three years (104 out of 138, Figure 2.2). Articles included study locations from 34 countries and all seven continents (Figure 2.3a), with most occurring in the United States of America (USA), Canada, and Australia (46, 14, and 13 respectively, Figure 2.3b). Studies were most frequently conducted in forests (93), followed by grassland (81), wetland (49), agriculture (7), and urban habitats (6, Figure 2.4).

In addition to a wide geographical range in study locations, our database of real and artificial nest studies included data representing 128 species in 44 families from 10 orders (Figure 2.5). Most of the species belonged to the Passeriformes (159), but also Charadriiformes (18), Anseriformes (11), and Galliformes (13). Open cup nests were the most common artificial nest type used (186 out of 224), and almost all of the artificial nests were the same nest type as the species of interest (210 out of 224). Artificial nests were most commonly placed in shrubs (104) or on the ground (93). Few studies placed nests in trees (15), such that the frequency of studies decreased as nest height increased (Figure 2.6).

When we examine the type of eggs used in the artificial nests, we see that real eggs were used in well over half of the study treatments (111 real only and 65 real and fake eggs), whereas artificial nests with only fake eggs were less common (45). Quail eggs were the eggs most commonly used (114), followed by chicken (39), finch (16), sparrow (6), and budgie (1) eggs (figure 2.7). Fake eggs were either clay (99) or wax (8, figure 2.7).

Clutch sizes were similar between real and artificial nests with four eggs being the most common real nest clutch size (89, figure 2.8a) and three eggs being the most common artificial nest clutch size (107, figure 2.8b). When the real and artificial clutch sizes were compared directly, we again found that number of eggs in a clutch was similar between studies (139 out of 225 studies had a difference less than or equal to one egg, figure 2.8c). In addition to possessing similar number of eggs in clutches, real and artificial nests also had similar clutch volumes (egg volume multiplied by clutch size). When relativized ((artificial – real clutch volume)/real clutch volume) most treatments possessed a relative difference less than or equal to 0.5 ml (figure 2.9). When we divide the clutch volume (ml) by the adult mass (g) to look at reproductive investment relative to adult body size, we see that most of the treatments have an investment of 0.3-0.4 ml/g (figure 2.10).

The most common incubation lengths for real nests were 12 days (53), 14 (28), 13 (17), 21 (17), 16 (15, figure 2.11a). Whereas for artificial nests the most common number of exposure days was 14 (41), 15 (29), and 12 (23), but exposure periods ranged from one to 34 days (figure 2.11b). When we directly compare the real incubation period versus the artificial exposure period for each study, the most common difference was zero days (95 out of 230), but again the range was -29 to 17 days difference (figure 2.11c). The investigator visitation rates varied widely between real and artificial nests. Real nests were primarily visited four or five times during the course of observation (33 and 24 treatments respectively, figure 2.12a), but artificial nests were often visited by researchers anywhere from two to seven times (38, 32, 40, 36, 18, and 22 treatments respectively, figure 2.12b).

The timing of the measure of success for real nests did vary widely across studies. Most of the treatments determined that real nests were successful when the nest hatched (104), but many treatments also specified that nests had to fledge nestling to be successful (87, figure 2.13). However, some studies were unclear when success was determined for real nests (34) and a few chose less standard periods to determine success. Some of the outlier treatments chose to observe nests for short periods of time (e.g., after three, four, or seven days of observation), but one treatment chose to specify the fourth day of incubation as the period when success was measured.

Questions and Treatment Summary

We divided the questions from the studies into six distinct categories based on the main objective of the study and treatments. Local habitat characteristics questions were the most studied (91), followed by nest characteristics (76), predators (26), real versus artificial (22), landscape characteristics (21), and methodology (9). The most common local habitat characteristic question treatment groups were associated with microhabitat characteristics in the area immediately surrounding nests (23), the density of vegetation (17), the distance to edge habitat/habitat patch edge (14), the density of nests (10), and whether nests were colonial vs solitary (6). In studies focused on nest characteristic questions, popular treatment groups were: the placement of nests (17), the substrate used in nest construction (15), the size of eggs (8), the type of egg used in artificial nests (7), and the amount of nest cover or concealment (7). The effects of predator removal (10) and the type of predators depredating nests (9) were the most common treatment groups for predator questions. Real and artificial nest questions were mostly treatment groups of real and artificial nests only (20). The treatment groups of landscape characteristic question studies were divided into island vs mainland patches (7), patch size (7), and fragmentation treatments (6). Studies investigating methodology questions were mainly focused on nest camera versus no nest camera treatments (6).

Meta-analysis Model Results

The sample sizes of complete data lines for our glmm models varied widely from 17 real nest treatments in the NSR nest visitation model to 128 artificial nest treatments in the ANS nest type model (Figure 2.14). The absolute latitude models were the only models where AIC selection favored an interaction between our nest covariate and covariate of interest. As a result, our absolute latitude predictions for both NSR and ANS indicate an increase in survival for real nests as absolute latitude increases whereas artificial nests experienced a decrease in survival as absolute latitude increases (Table 1.1, Figure 2.15). When we examine the predictions for the nest size models we see that the real and artificial nests both exhibit increases in predicted NSR as nest size increases, with artificial nests consistently having lower survival (Table 1.2, Figure 2.16a). Whereas, artificial and real nests exhibit nearly the same predicted ANS and decline in survival as nest size increases (Table 1.2, Figure 2.16b). As the number of nest visits by investigators increased, the predicted survival of nests decreased for real and artificial nests in both NSR and ANS models, with artificial nest survival consistently lower than real nest survival (Table 1.3, Figure 2.17). For our analysis of the effects of our categorical covariates, we consistently observed a lower predicted survival rate for artificial nests versus real nests in NSR and ANS analyses. For habitat type, we found that NSR and ANS models possessed different patterns, but artificial nests consistently had lower survival than real nests (Table 1.4, Figure 2.18). When we examine the effects of nest type, we see similar trends between NSR and ASN with survival slightly lower for artificial nests versus real nests (Table 1.5, Figure 2.19). However, nest placement also possessed different patterns for ANS and NSR, but artificial nests still had lower survival than real nests (Table 1.6, Figure 2.20).

DISCUSSION

Overall, across nearly all of the continuous gradients and within the many categorical groups that we examined, predicted survival for artificial nests was lower than predicted survival for real nests, but the difference was mostly insignificant. While individual studies may exhibit some variation, the diversity in species (n = 128), habitats (n = 5), and locations (7 continents and 34 countries) of the studies we incorporated into our meta-analysis creates strong support for the pattern of slightly lower predicted survival for artificial nests than real nests, which indicates that the pattern applies across systems and species. Lower survival for artificial nests aligns with the theory that artificial nests have lower survival than real nests due to a lack of parental protection (Zanette 2002; Komdeur and Kats 1999; Wilson, Brittingham, and Goodrich 1998; Davison and Bollinger 2000).

In addition to consistently exhibiting lower predicted survival in almost all of our models, artificial nests exhibited the same predicted survival pattern as real nests in almost all of our models. Again, indicating that artificial nests are a valuable tool that can improve our understanding of how predation risk shapes avian systems. For absolute latitude, the model where the survival patterns were dissimilar between the real and artificial nests, we can explain opposite patterns in survival with a couple of theories. First, life history strategies may be the mechanism behind the opposing survival patterns. Where we would predict that parents use more cautious life history strategies and invest less into nests (e.g., locations closer to the equator) artificial nests have greater predicted survival than real nests, whereas in locations where parents invest heavily in nests and possess short life history strategies survival for real nests is greater than artificial nests (Thomas E. Martin 1996; Roper, Sullivan, and Ricklefs 2010). Alternatively, the specialization of predator communities as absolute latitude decreases may drive the observed divergence. As predators become more specialized in lower latitudes, it is likely that artificial nests placed by researchers are outside of their niche and therefore are only (Schall and Pianka 1978).

Although we find that artificial nests appear to adequately represent at least nest predation risk, we found that the metric used to analyze survival influenced the survival trend observed across our covariates of interest. The differences in patterns of predicted survival varied unpredictably between the two survival metrics. For nest size, nest type, and nest placement the trends in survival were opposite between the NSR and ANS survival predictions, whereas absolute latitude, nest visit, and habitat type had similar trends for NSR and ANS model predictions. The tendency for variation between NSR and ANS trends in predicted survival indicates that comparisons between the two survival metrics may lead to misleading results. Articles that compare the survival of real and artificial nests in two different survival metrics (e.g., real nests were commonly reported in NSR whereas artificial nests were most commonly reported in ANS, Figure 2.14) may therefore exhibit unpredictable differences in the survival of real and artificial nests due to inconsistencies based upon the survival metrics used rather than the actual variation in survival between the two types of nests.

The similarity between artificial and real nest survival that we observed may reflect the quality of studies we included in our analysis. We chose to use a paired approach where artificial and real nest results were from the same study to reduce variation that may result from differences in geographic location, research methods used, and other potentially confounding variables. In addition to selecting articles with paired data, the studies used were of high quality because investigators appeared to make considerable effort to create artificial nests similar to the real nests they imitated. The majority of studies used real eggs (176 of 221), mimicked the same nest type (211 of 225), and placed nests in similar locations (206 of 213). Nest predators form search images based on prey appearance and location (Thomas E. Martin 1993; Gendron 1986; Dukas and Kamil 2001), thus, ensuring that nests were in similar locations and possessed similar appearances could have greatly contributed to the similar survival results we observed between real and artificial nests. However, researchers did not always concentrate on exposing artificial nests for similar periods (95 of 230), introducing a greater amount of variation with the exposure periods for real and artificial nests. In addition to variation in exposure days between real and artificial nests, there was also variation in when real nests were determined to be successful (104 treatments measured success when nests hatched and 87 treatments measured success when nests fledged). The survival of incubated eggs and nestlings varies for real nests (Grant et al. 2005; Stake 2003), so it stands to reason that artificial nests with eggs are an inadequate replications of real nests with nestlings. We attempted to counteract this issue by calculating NSR based on the incubation period only, but for some ANS studies survival data for incubation exclusively was unavailable.

The increase in the number of articles published and improvements in accessibility of articles has improved the ability of researchers to conduct meta-analyses that allow science to evaluate methods and investigate large-scale questions. However, the lack of reporting basic summary statistics and the inconsistency in how survival results are reported for nest studies creates many issues for meta-analyses. Researchers need to present sample sizes for treatment groups when results are reported. In numerous articles, sample sizes were reported in the methods section, but not included in figures with multiple treatments, creating uncertainty as to the actual number of nests that were included in each group. Also, some articles failed to report background information on study species and sampling methods, creating issues with missing data. Consistently reporting sample sizes for all treatment groups independently, incubation/exposure periods, nest type/placement information, and longitude/latitude of the research location would improve the quality of future meta-analyses. In addition to issues with reporting background information, inconsistencies in reporting survival in the same metric eliminated several articles from inclusion in our meta-analysis. Within a single article survival should always be presented in the same metric (particularly when comparisons are being made), but to improve the ability of future meta-analyses to be conducted more standardized reporting of at least ANS (preferably both ANS and NSR) must occur.

CONCLUSION

Artificial nests consistently exhibited insignificantly lower predicted survival rates than real nests, and displayed similar patterns of survival in 10 out of our 12 glmm models, indicating that artificial nests are likely a useful tool for improving our understanding of avian systems, if applied correctly. The diversity in species, methods, and locations studied supports the conclusion that the pattern of consistent differences in real and artificial nest survival that we observed can be applied widely across systems. However, the survival metric used to analyze nest survival appears to influence the patterns of nest survival observed. Thus, when comparing the survival of artificial and real nests, researchers should be cautious of comparing survival results using different survival metrics. In the future, more consistent reporting of sample sizes, background information, and survival results in similar metrics will improve our ability to do large-scale comparisons and improve the quality of future meta-analyses.

TABLES AND FIGURES

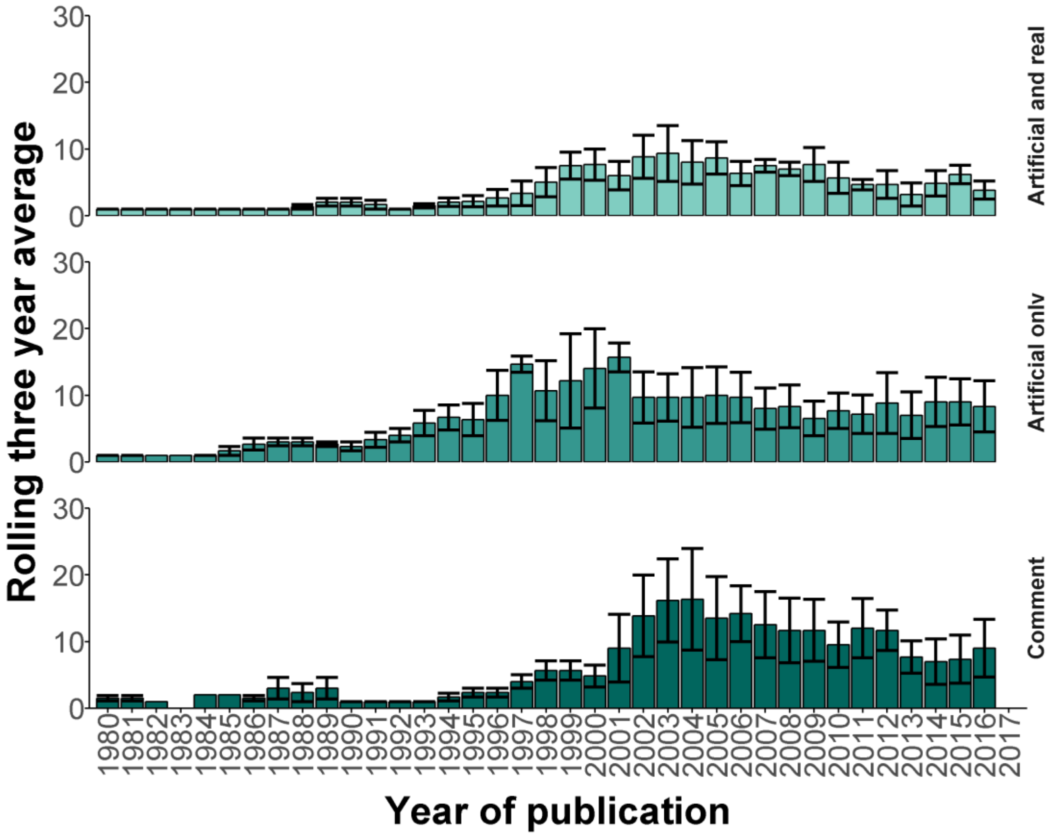

Figure 1. 1 The use of artificial nests became popular in the late 1980s, but the use of real and artificial nests in articles did not increase until the late 1990s. Following the increase in artificial nest use, articles mentioning artificial nests increased greatly in the 1990s. The graph below depicts the three year rolling average of the number of articles published each year that either used only artificial nests in experiments (Artificial only), used artificial and real nests in experiments (Artificial and real), or mentioned artificial nests (Comment).

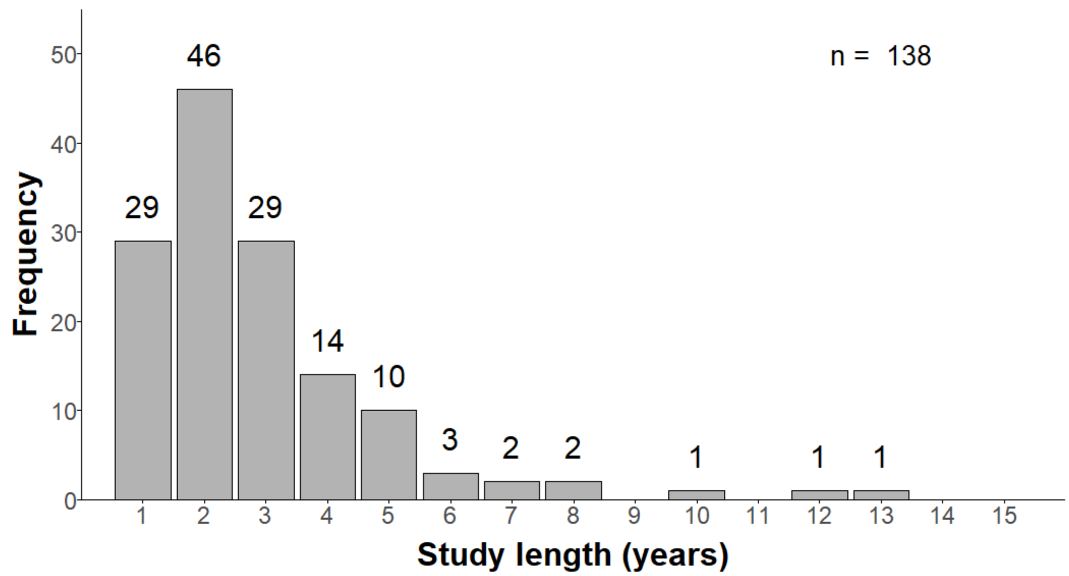

Figure 1. 2 The majority of the articles in our meta-analysis had a study length less than or equal to three years (104 out of 138).

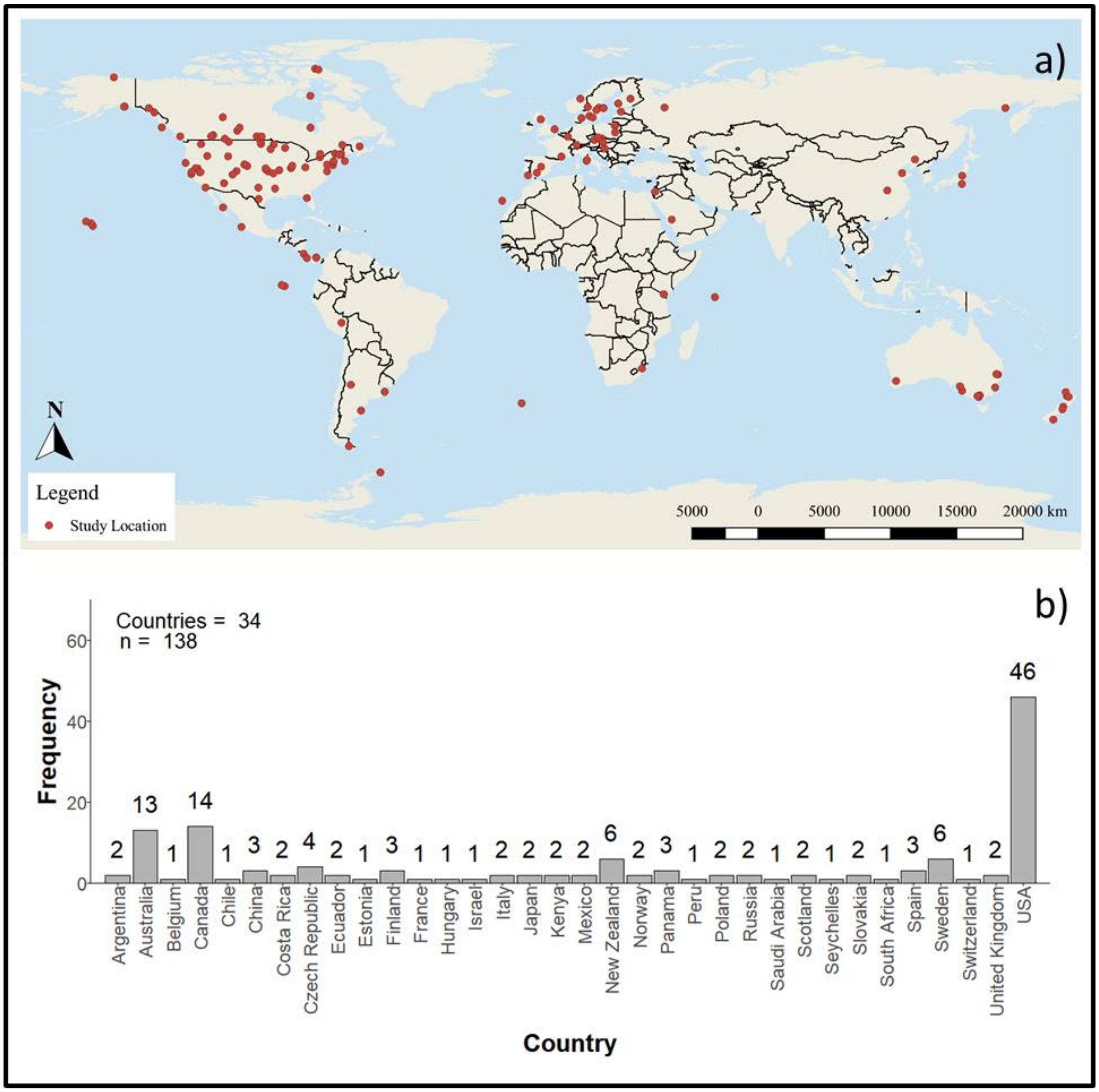

Figure 1. 3 Articles included locations from all seven continents (a), and 34 countries (b). Most of the articles were from the United State of America (USA, 45), but Canada (14), Australia (13), New Zealand (6), and Sweden (6) also had more than five articles.

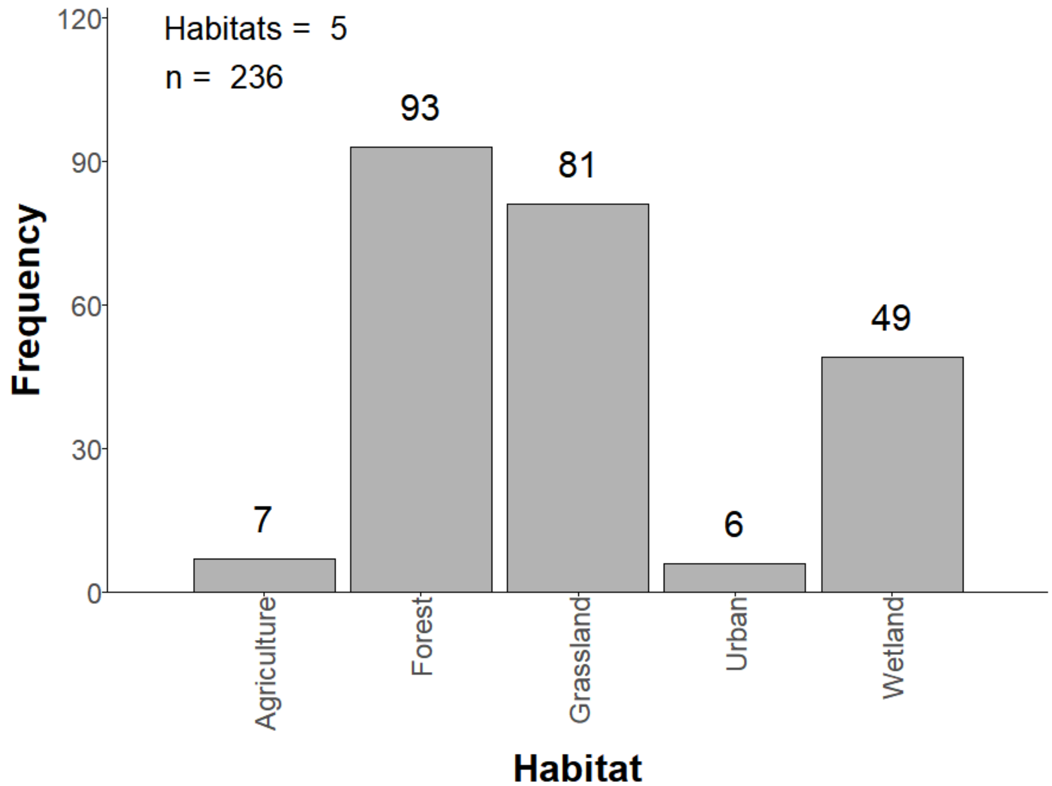

Figure 1. 4 Forests and grasslands were the most commonly studied habitat types, followed by wetlands. Agriculture and urban habitats were excluded from analyses due to limited sample sizes.

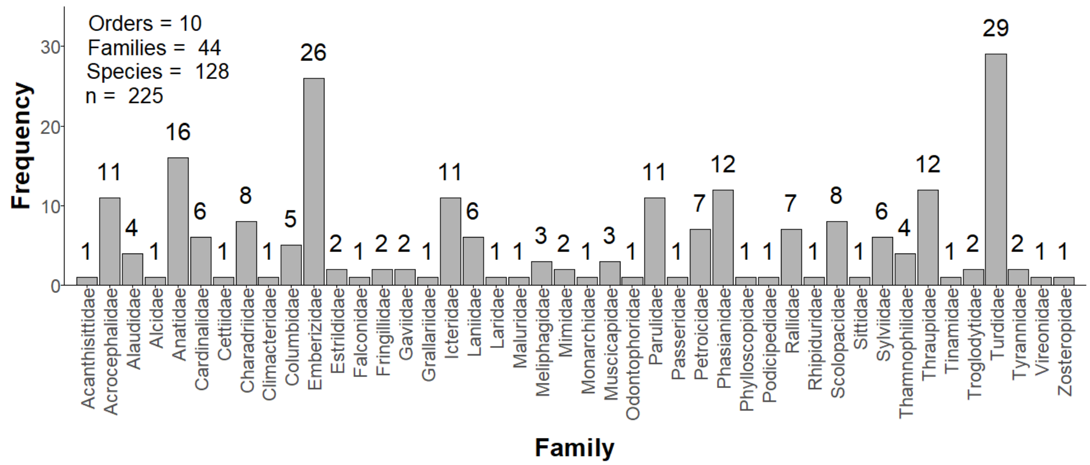

Figure 1. 5 Studies included 128 species from 44 unique families representing 10 orders. The primary orders included: Passeriformes (159), Charadriiformes (18), Anseriformes (11), and Galliformes (13).

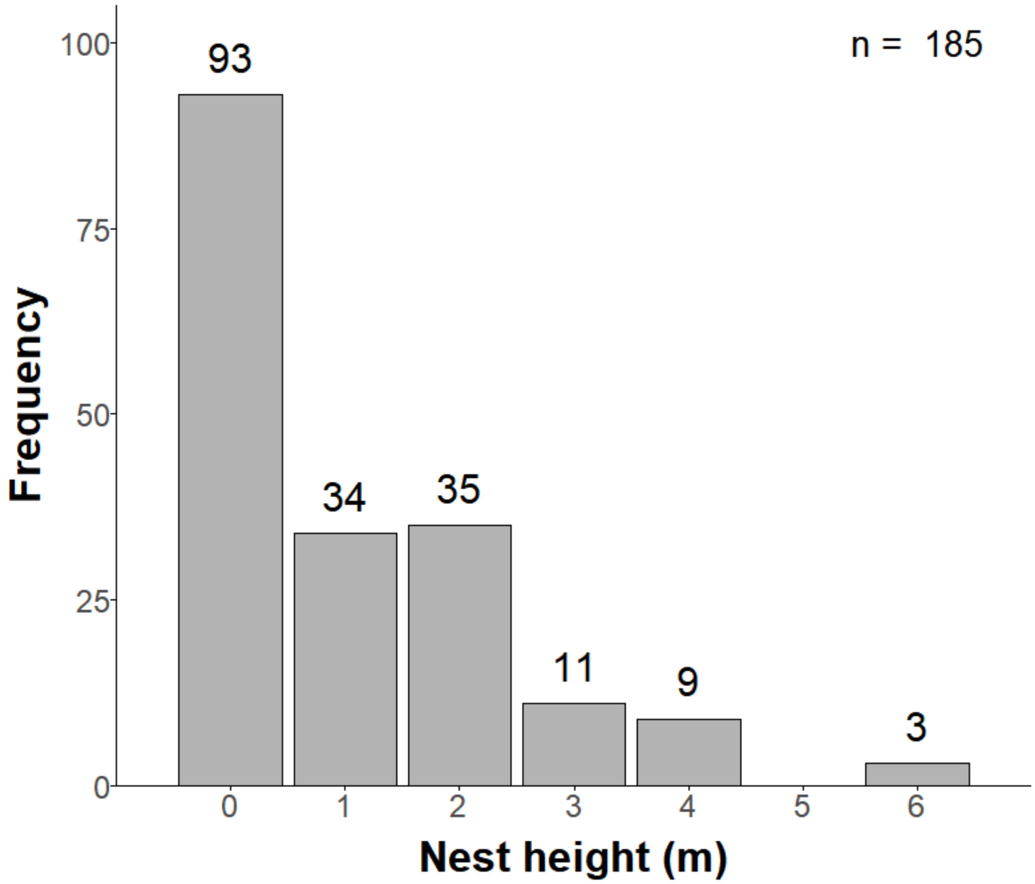

Figure 1. 6 Most artificial nests were placed on the ground or in shrubs, resulting in a decrease in frequency as nest height increases.

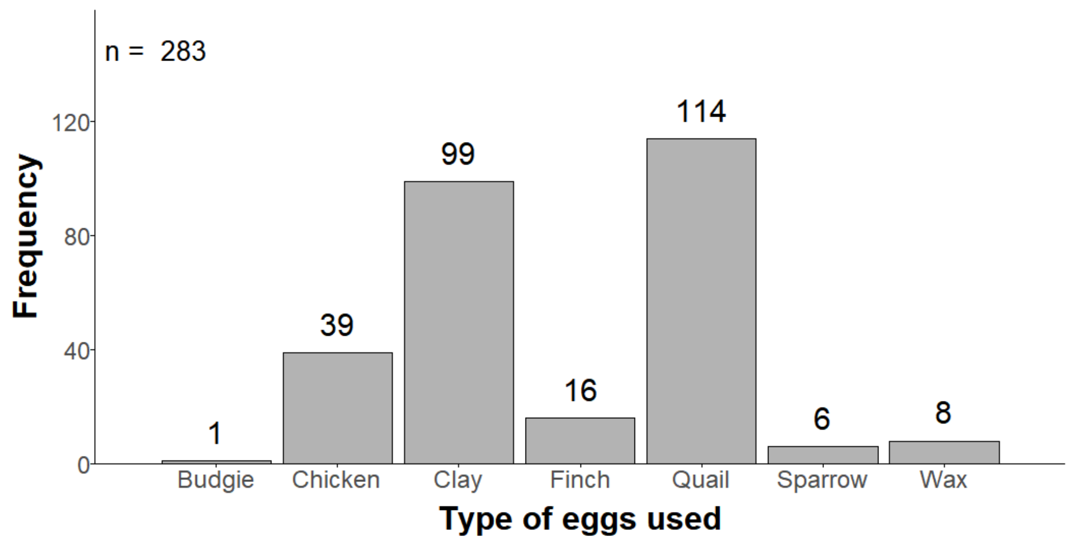

Figure 1. 7 Quail eggs were the most commonly used egg type in artificial nests. Clay eggs were the most common fake egg type used in artificial nests.

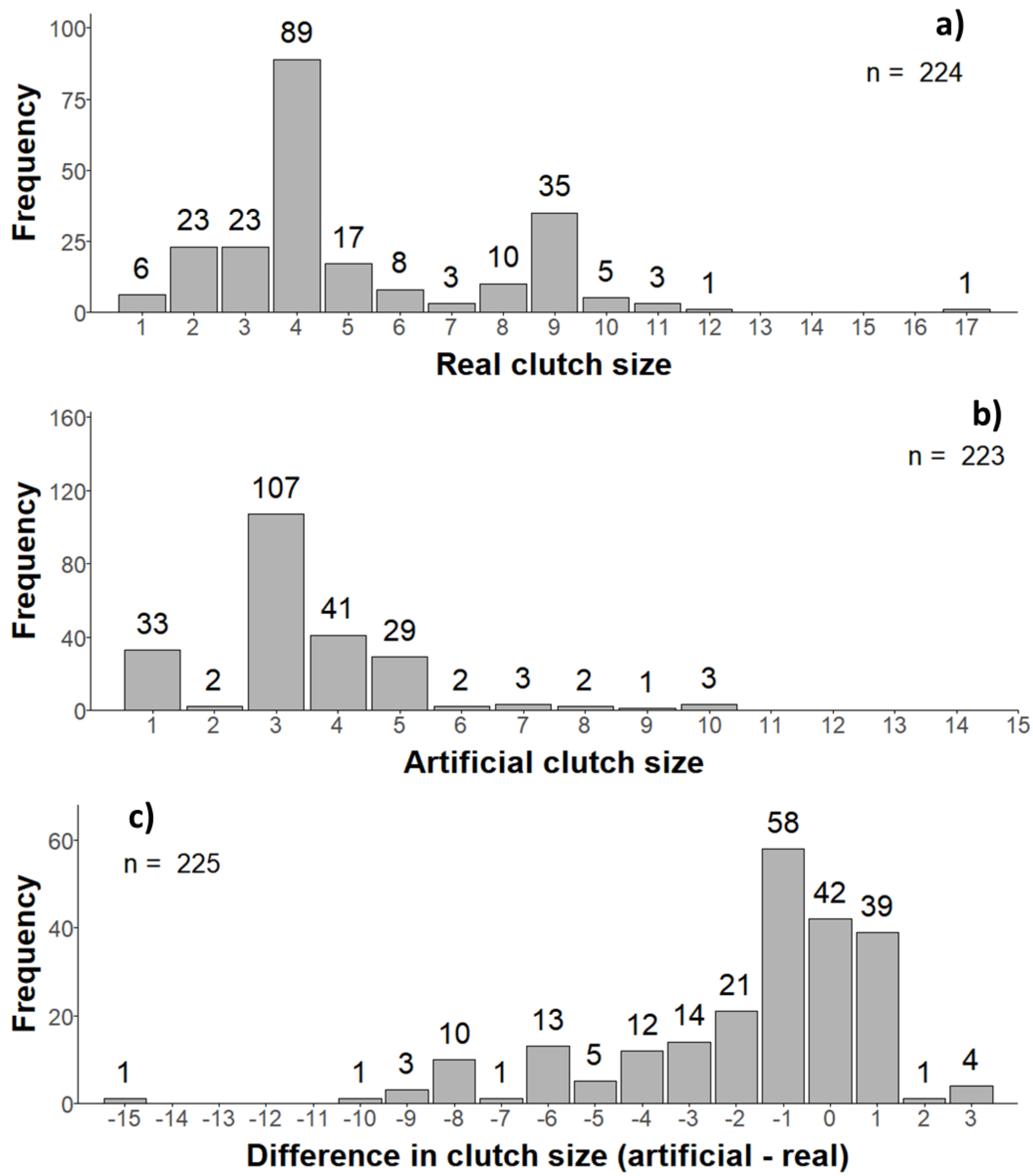

Figure 1. 8 Real and artificial nests had similar clutch sizes. For real nests, an average clutch of four eggs was most common (a), and three eggs were most commonly used in artificial nests (b). Within most studies, an absolute difference in clutch size less than or equal to one egg was observed (c).

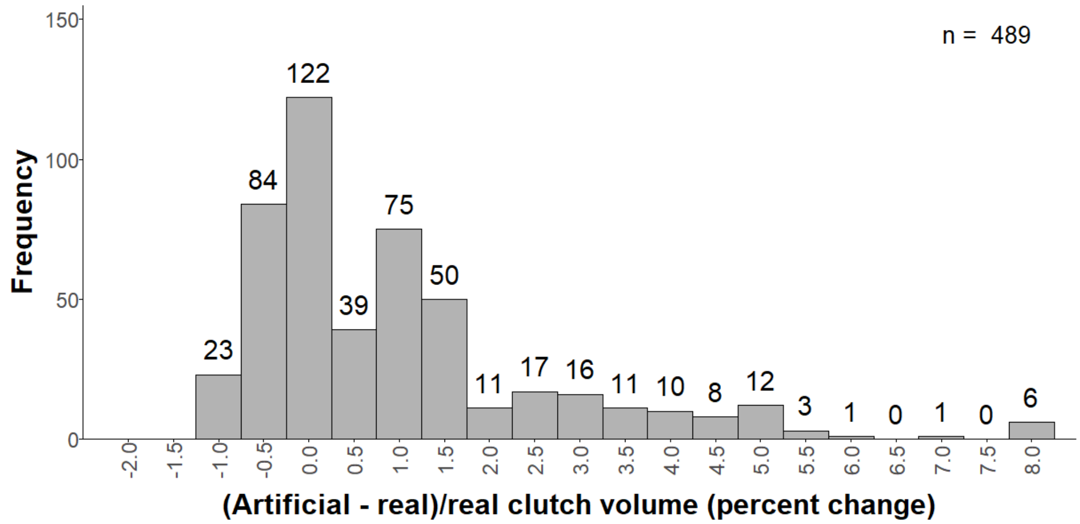

Figure 1. 9 When the difference in total volume of the clutch was relativized by the total clutch volume of real nests, most treatments possessed a relative difference less than or equal to 0.5 ml.

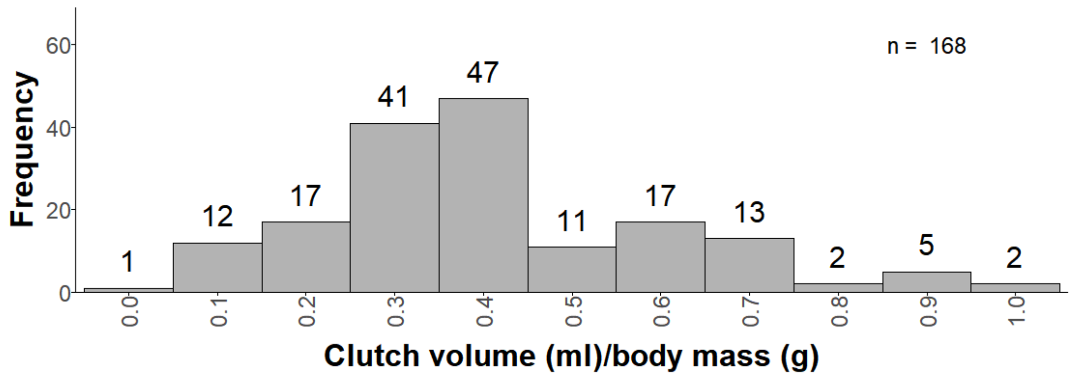

Figure 1. 10 Reproductive investment was normally distributed around a mean of 0.4 ml/g, based on total clutch volume divided by adult body mass.

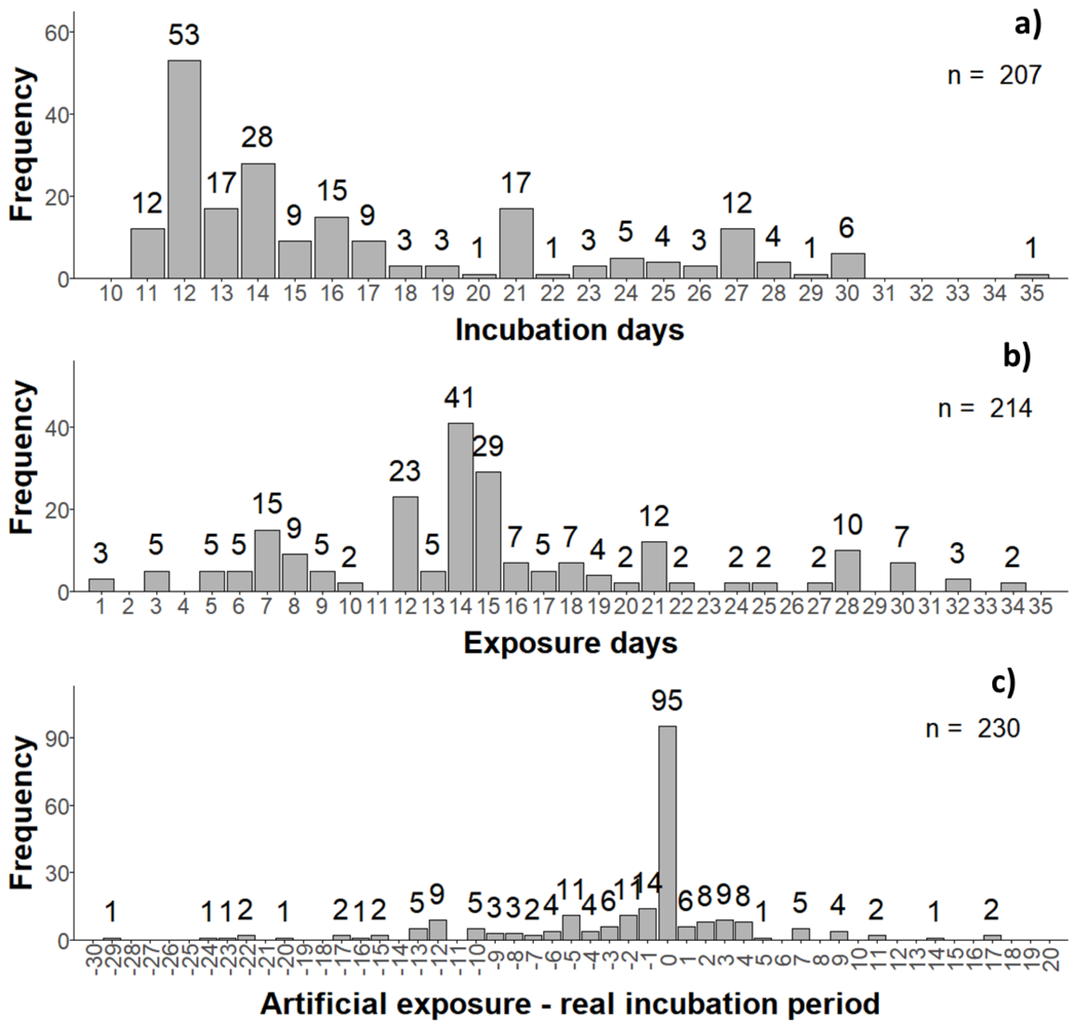

Figure 1. 11 The most common incubation lengths for real nests were 12, 14, 13, 21, and 16 days (a). Whereas for artificial nests, the most common number of exposure days was 14, 15, and 12, but exposure periods ranged from one to 34 days (b). When we directly compared the real incubation period versus the artificial exposure period for each study, the most common difference was zero days, but again the range was -29 to 17 days difference (c).

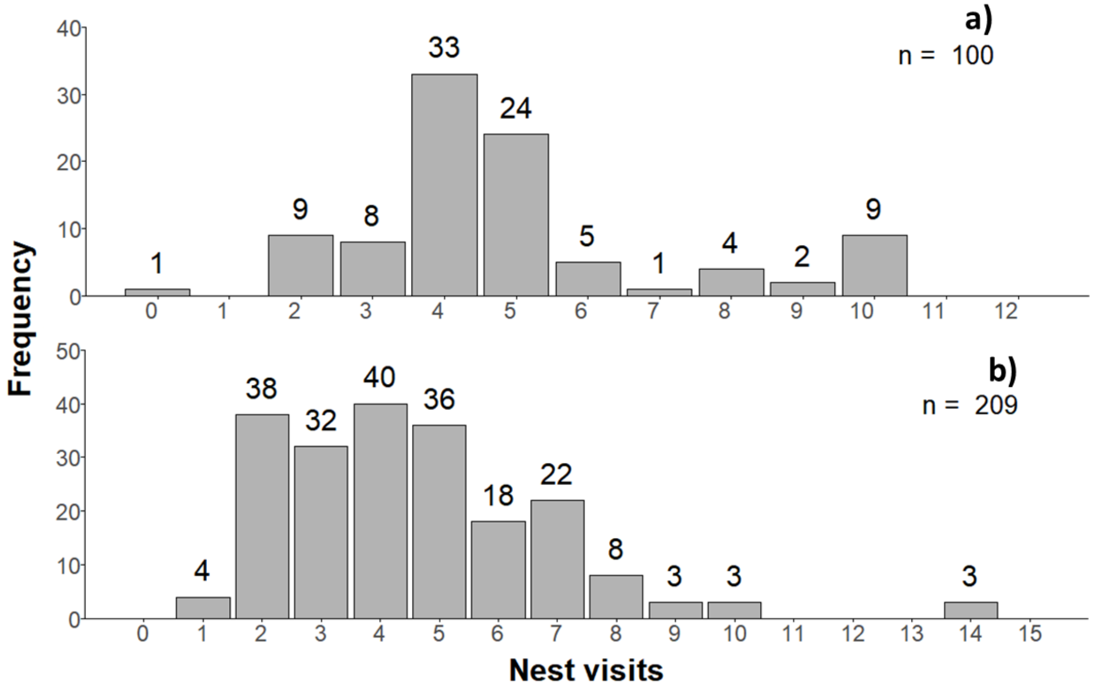

Figure 1. 12 Real nests were most commonly visited four or five times by investigators (a), whereas artificial nests were commonly visited anywhere from two to seven times (b). However, many studies failed to report how many times real nests were visited.

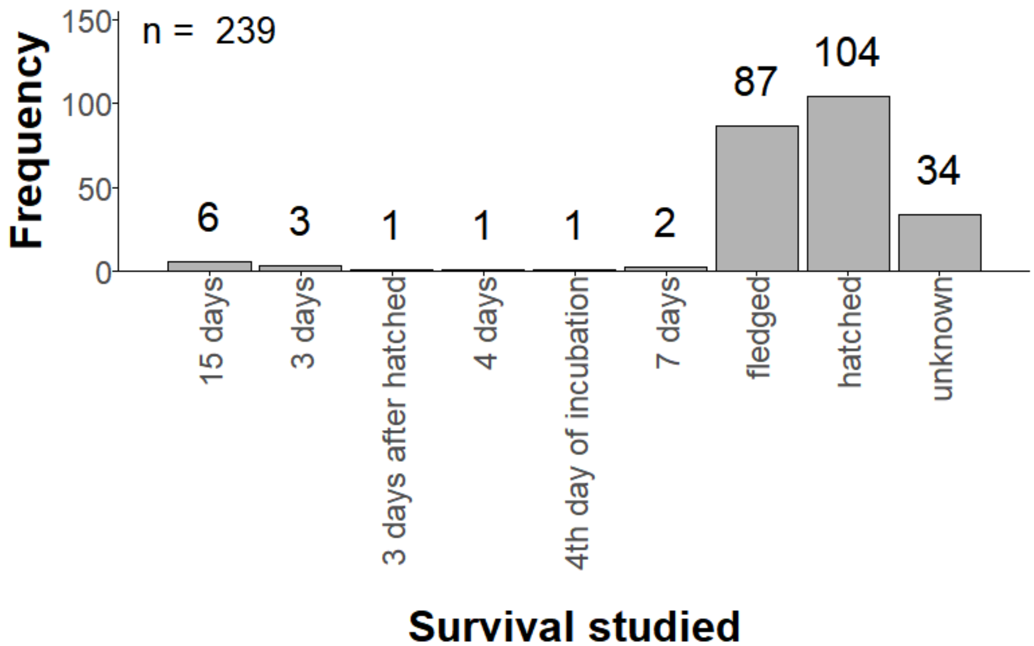

Figure 1. 13 Most studies recorded real nests as successful if eggs hatched, but many recorded success at fledging. However, 34 studies did not specify when success was recorded and some used less standard periods.

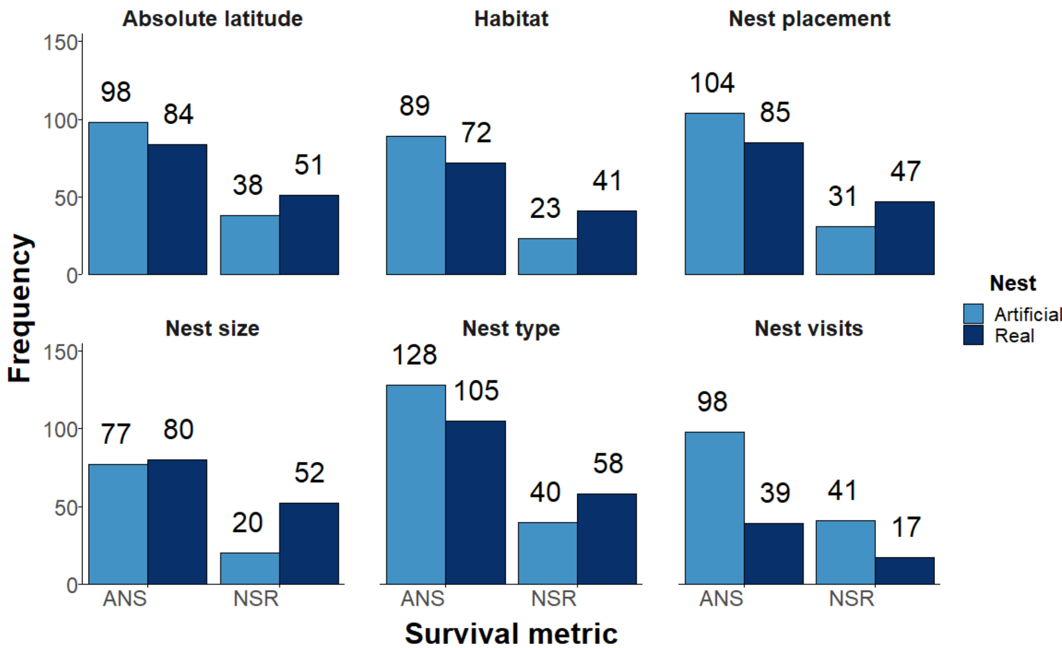

Figure 1. 14 The apparent nest success (ANS) models possessed larger sample sizes than the nest survival rate (NSR) models in each model set. Artificial nests had greater ANS sample sizes than real nests, and real nests had greater NSR sample sizes than artificial nests. Overall, sample sizes ranged from 17 to 128 treatments.

Table 1. 1 Coefficient estimates from the absolute latitude generalized linear mixed effects models. The models included absolute latitude as the variable of interest, along with nest (whether the survival data was from real or artificial nests), the placement of the nest (either ground or shrub), and the number of days nests were exposed as fixed effects. The interaction between absolute latitude and nest was positive in both the nest survival rate and apparent nest success models because the confidence intervals were entirely positive.

	Estimate	**SE**	**Lower 95% CI**	**Upper 95% CI**
Nest Survival Rate				
Intercept*	-1.7479	0.6076	-2.9389	-0.5570
Absolute latitude	-0.6237	0.5300	-1.6625	0.4150
Nest(Real)*	1.3300	0.5391	0.2734	2.3867
Nest placement(Shrub)	0.7439	0.5773	-0.3876	1.8753
Exposure days	-0.1903	0.3308	-0.8386	0.4581
Absolute latitude*Nest(Real)*	1.4756	0.6325	0.2360	2.7152
Apparent Nest Success				
Intercept	-0.0439	0.2726	-0.5781	0.4904
Absolute latitude	-0.1458	0.2066	-0.5509	0.2592
Nest(Real)	0.3395	0.3109	-0.2698	0.9489
Nest placement(Shrub)	-0.0733	0.3480	-0.7554	0.6089
Exposure days	-0.2662	0.1792	-0.6175	0.0850
Absolute latitude*Nest(Real)*	0.7181	0.3342	0.0630	1.3732

**Variables that possess 95% confidence intervals that do not overlap zero.*

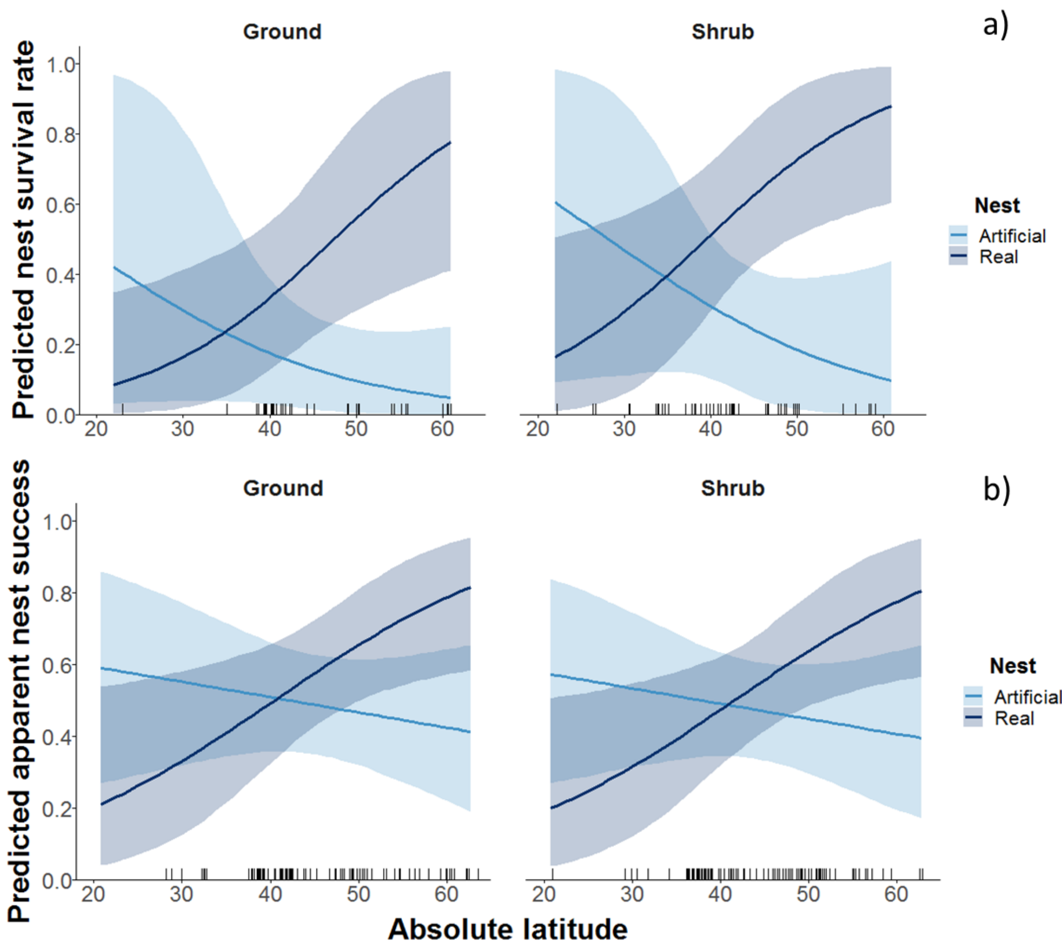

Figure 1. 15 Artificial and real nest predicted survival patterns were opposite for both the nest survival rate (NSR, a) and apparent nest success (ANS, b) models. The difference in survival patterns may be the result of predation risk and parent life history strategies. In lower latitudes parents exhibit slow life history strategies with lower investment in offspring, which may cause artificial nests to have greater survival due to no parental cues attracting predators to nests. Whereas at higher latitudes parents exhibit short life history strategies with greater investments in offspring, so a lack of parental protection decreases artificial nest survival. The tally marks at the bottom of each graph represent the distribution of data.

Table 1. 2 Coefficient estimates from the clutch volume generalized linear mixed effects models. The models included clutch volume (egg volume * average number of eggs in a clutch) as the variable of interest, along with nest (whether the survival data was from real or artificial nests), the placement of the nest (ground or shrub), and the number of days nests were exposed as fixed effects. None of the estimates possessed statistically significant effects because all estimate confidence intervals overlapped zero.

	Estimate	**SE**	**Lower 95% CI**	**Upper 95% CI**
Nest Survival Rate				
Intercept	-1.5366	0.7865	-3.0781	0.0049
Nest volume	0.4441	0.3405	-0.2233	1.1115
Nest(Real)	1.3466	0.7594	-0.1419	2.8350
Nest placement(Shrub	0.4414	0.5839	-0.7031	1.5858
Exposure period	-0.1420	0.2929	-0.7161	0.4322
Apparent Nest Success				
Intercept	0.2847	0.3982	-0.4957	1.0652
Nest volume	-0.2397	0.2178	-0.6666	0.1872
Nest(Real)	0.0298	0.4791	-0.9092	0.9689
Nest placement(Shrub	-0.2107	0.3877	-0.9706	0.5492
Exposure period	-0.2101	0.1959	-0.5940	0.1738

**Variables that possess 95% confidence intervals that do not overlap zero.*

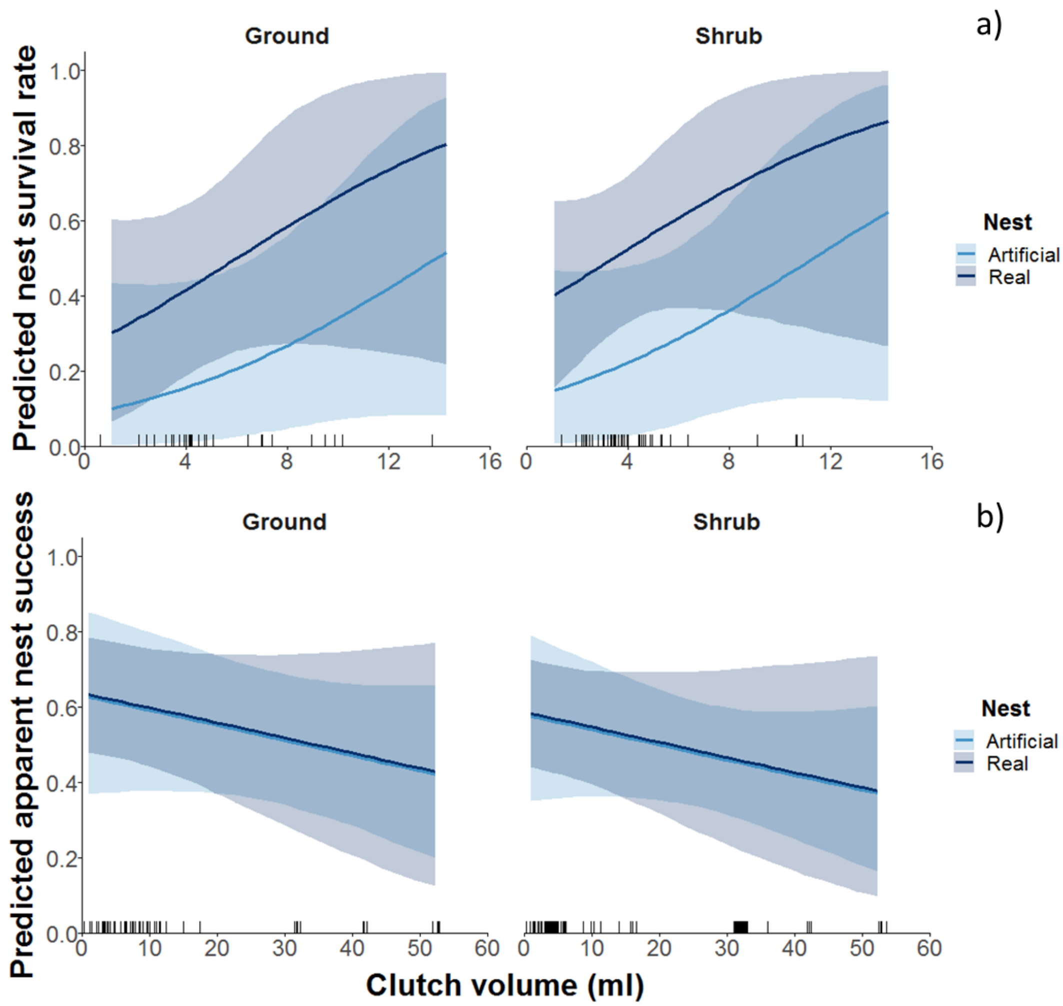

Figure 1. 16 The survival trends for nest survival rate (NSR, a) and apparent nest success (ANS, b) model were opposite for nest placement models. Artificial nests had slightly lower predicted survival in both sets of models, but the difference was not significant. Nest placement did not change survival trends or differences between real and artificial nests. The tally marks at the bottom of each graph represent the distribution of data.

Table 1. 3 Coefficient estimates from the nest visit generalized linear mixed effects models. The models included the number of nest visits by researchers as the variable of interest, along with nest (whether the survival data was from real or artificial nests), the placement of the nest (ground or shrub), and the number of days nests were exposed as fixed effects. When the estimate confidence intervals did not overlap zero, we determined that the estimates possessed a statistically significant effect on nest survival (either positive or negative base on sign).

	Estimate	**SE**	**Lower 95% CI**	**Upper 95% CI**
Nest Survival Rate				
Intercept*	-3.2988	1.0981	-5.4511	-1.1466
Nest visits	-0.5180	0.3836	-1.2698	0.2339
Nest(Real)	0.6267	0.6732	-0.6927	1.9462
Nest placement(Shrub)*	2.7624	1.1424	0.5234	5.0014
Exposure period	0.2388	0.4281	-0.6002	1.0779
Apparent Nest Success				
Intercept	-0.0564	0.3012	-0.6467	0.5340
Nest visits	-0.1037	0.1769	-0.4505	0.2430
Nest(Real)	0.7010	0.3991	-0.0812	1.4832
Nest placement(Shrub	-0.1318	0.3949	-0.9058	0.6423
Exposure period*	-0.4262	0.2063	-0.8305	-0.0219

**Variables that possess 95% confidence intervals that do not overlap zero.*

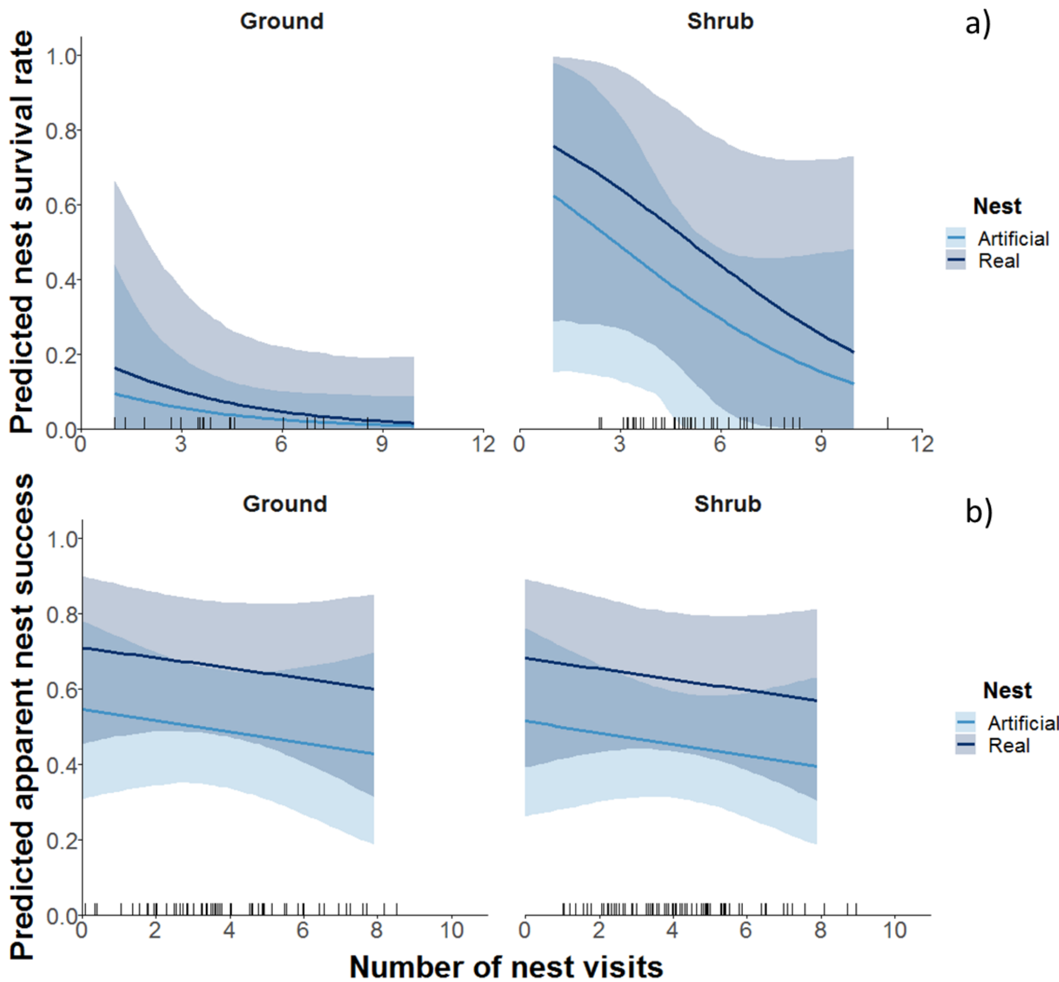

Figure 1. 17 As the number of times investigators visited nests increased, the predicted survival of nests decreased for both real and artificial nests in our nest survival rate (NSR, a) and apparent nest success (ANS, b) models. The decrease in ANS model predicts was less extreme than the decrease in NSR models, but the NSR predictions (ground nests in particular) were based on the smallest sample size. The predicted survival of artificial nests was slightly lower than real nest predicted survival for all nest visit models. The tally marks at the bottom of each graph represent the distribution of data.

Table 1. 4 Coefficient estimates from the habitat type generalized linear mixed effects models. The models included habitat type (forest, grassland, or wetland) as the variable of interest, along with nest (whether the survival data was from real or artificial nests), the placement of the nest (ground or shrub), and the number of days nests were exposed as fixed effects. When the estimate confidence intervals did not overlap zero, we determined that the estimates possessed a statistically significant effect on nest survival (either positive or negative base on sign).

	Estimate	**SE**	**Lower 95% CI**	**Upper 95% CI**
Nest Survival Rate				
Intercept*	-1.3473	0.6138	-2.5503	-0.1443
Exposure days	0.0756	0.2941	-0.5009	0.6521
Nest(Real)*	1.0809	0.5069	0.0874	2.0744
Habitat(Grassland)	-0.2925	0.6199	-1.5076	0.9226
Habitat(Wetland)	-0.0668	0.7320	-1.5015	1.3679
Nest placement(Shrub)	0.5548	0.5390	-0.5017	1.6113
Apparent Nest Success				
Intercept	-0.4468	0.3628	-1.1580	0.2643
Exposure days	-0.3810	0.1947	-0.7627	0.0007
Nest(Real)	0.3435	0.3328	-0.3087	0.9957
Habitat(Grassland)	0.5277	0.4030	-0.2621	1.3175
Habitat(Wetland)*	0.8728	0.4150	0.0594	1.6862
Nest placement(Shrub)	-0.2503	0.3725	-0.9805	0.4798

**Variables that possess 95% confidence intervals that do not overlap zero.*

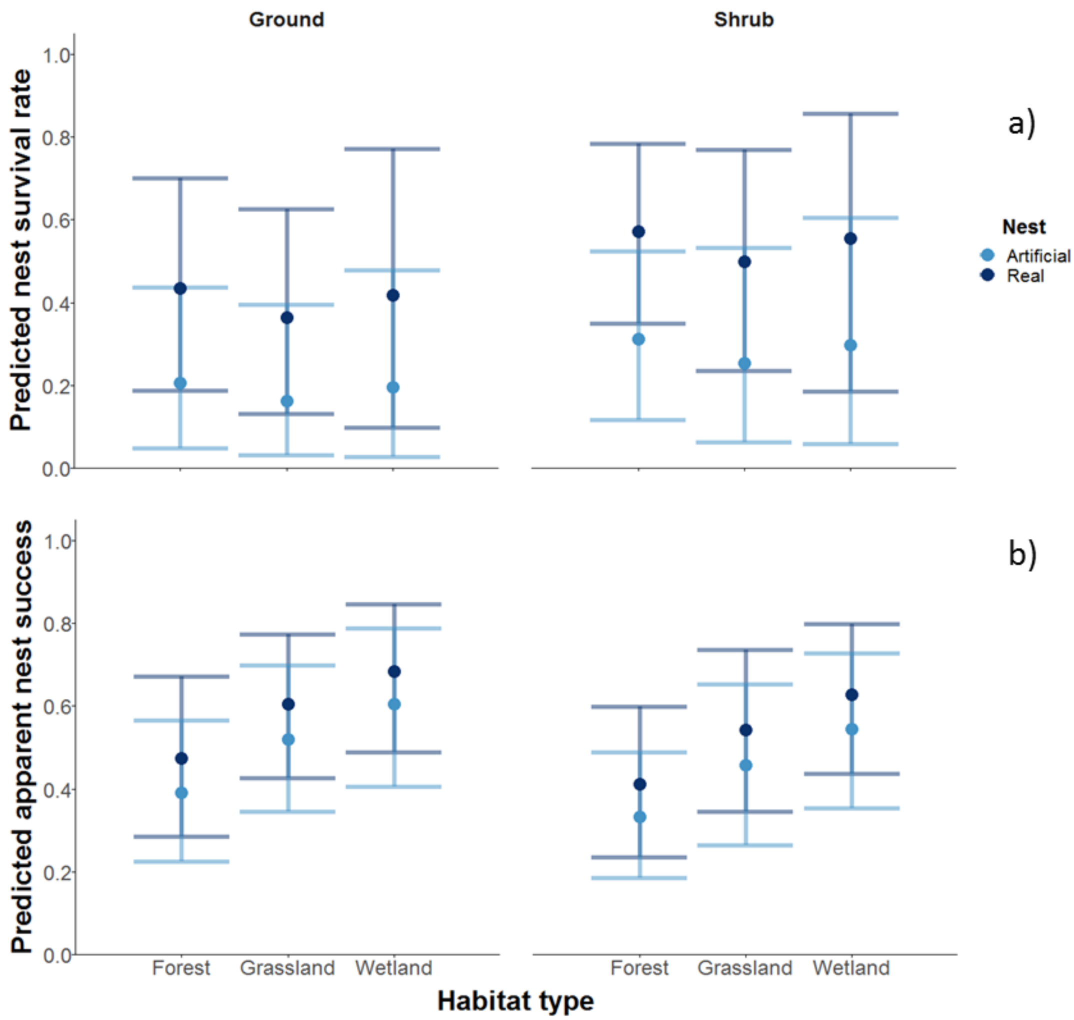

Figure 1. 18 Habitat type possessed a smaller influence on nest survival in our nest survival rate model (NSR, a) than our apparent nest success model (ANS, b). Whereas, nest placement minimally influenced nest survival. Across all predictions, artificial nests possessed the same survival pattern with slightly lower survival than real nests.

Table 1. 5 Coefficient estimates from the nest type generalized linear mixed effects models. The models included nest type (open cup, closed cup, and scrape) as the variable of interest, along with nest (whether the survival data was from real or artificial nests), the placement of the nest (ground or shrub), and the number of days nests were exposed as fixed effects. When the estimate confidence intervals did not overlap zero, we determined that the estimates possessed a statistically significant effect on nest survival (either positive or negative base on sign).

	Estimate	**SE**	**Lower 95% CI**	**Upper 95% CI**
Nest Survival Rate				
Intercept	-0.9384	1.2083	-3.3067	1.4298
Exposure days	0.0743	0.2247	-0.3661	0.5146
Nest(Real)*	0.8899	0.4181	0.0704	1.7094
Nest type (Open cup)	-0.4107	1.1002	-2.5670	1.7457
Nest type (Scrape)	0.2181	1.2606	-2.2527	2.6888
Nest placement(Shrub)	0.4356	0.4856	-0.5162	1.3875
Apparent Nest Success				
Intercept	-0.0704	0.4793	-1.0099	0.8691
Exposure days	-0.1783	0.1558	-0.4835	0.1270
Nest(Real)	0.4069	0.2724	-0.1271	0.9408
Nest type (Open cup)	-0.0489	0.4648	-0.9599	0.8622
Nest type (Scrape)	-1.0137	0.6671	-2.3213	0.2939
Nest placement(Shrub)	-0.0904	0.3050	-0.6882	0.5074

**Variables that possess 95% confidence intervals that do not overlap zero.*

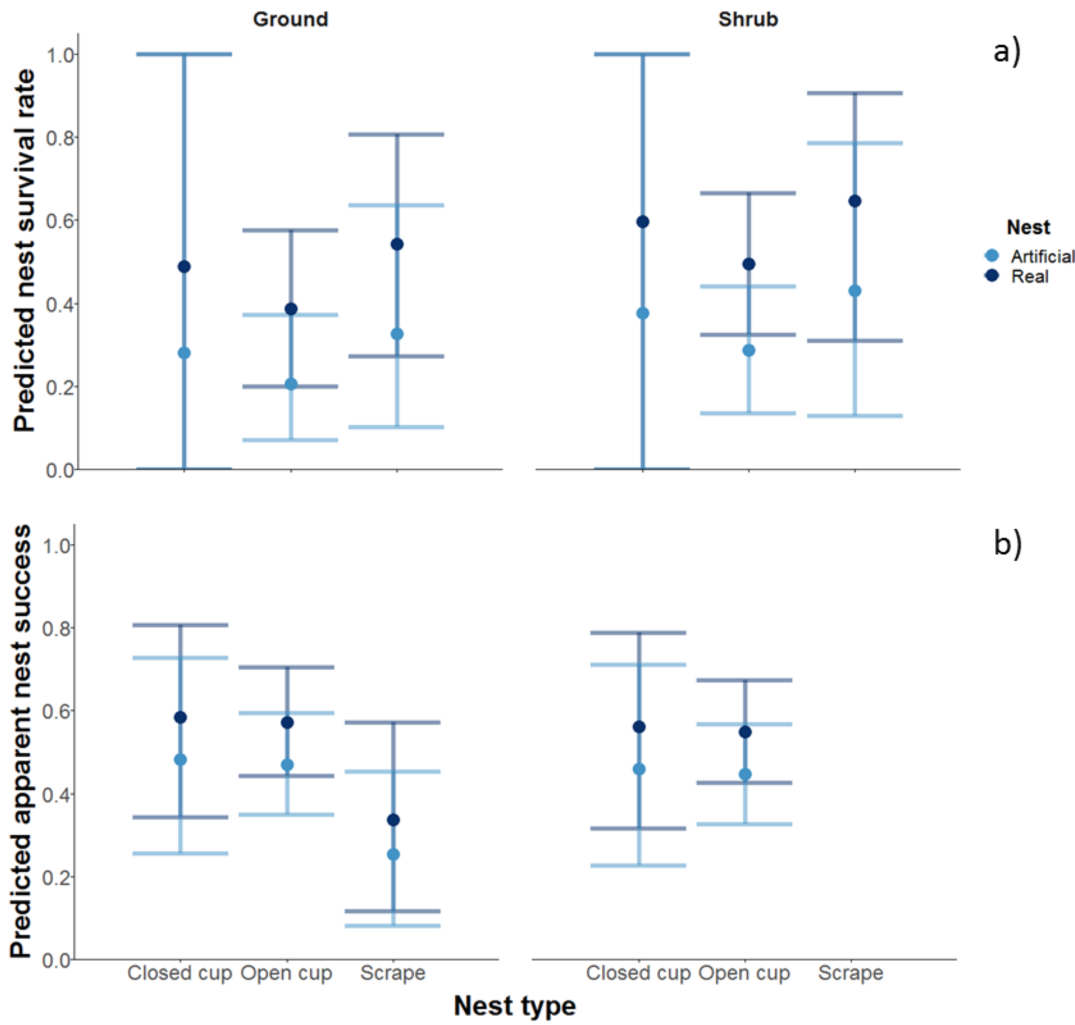

Figure 1. 19 Nest type did not influence the overall trend in predicted survival, but it did influence nest survival predictions. The nest survival rate model (NSR, a) and apparent nest success model (ANS, b) exhibited similar results. Overall, artificial nest survival exhibited the same pattern as real nests, but had slightly lower predicted survival.

Table 1. 6 Coefficient estimates from the nest placement generalized linear mixed effects models. The models included nest placement (ground or shrub) as the variable of interest, along with nest (whether the survival data was from real or artificial nests) and the number of days nests were exposed as fixed effects. When the estimate confidence intervals did not overlap zero, we determined that the estimates possessed a statistically significant effect on nest survival (either positive or negative base on sign).

	Estimate	**SE**	**Lower 95% CI**	**Upper 95% CI**
Nest Survival Rate				
Intercept*	-1.5408	0.5445	-2.6081	-0.4735
Exposure days	0.0667	0.2557	-0.4345	0.5679
Nest(Real)*	1.1001	0.4777	0.1637	2.0365
Nest placement(Shrub)	0.4953	0.5193	-0.5225	1.5131
Apparent Nest Success				
Intercept	-0.0599	0.2658	-0.5808	0.4611
Exposure days	-0.2724	0.1723	-0.6101	0.0652
Nest(Real)	0.4145	0.3008	-0.1751	1.0040
Nest placement(Shrub)	-0.1775	0.3367	-0.8374	0.4825

**Variables that possess 95% confidence intervals that do not overlap zero.*

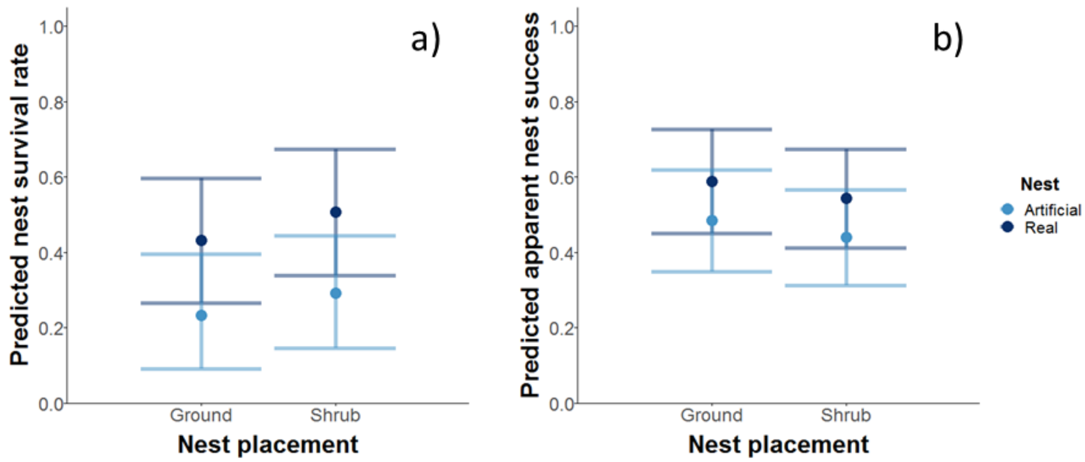

Figure 1. 20 Nest placement did not influence predicted nest survival or the pattern of survival. The nest survival rate model (NSR, a) and the apparent nest success model (ANS, b) exhibit similar patterns. Across all nest placement models, artificial nests possessed the same pattern as, but slightly lower predicted survival than, the real nests.

CHAPTER 2: EXAMINING THE EFFECTS OF PATCH SIZE AND NEST DENSITY ON ARTIFICIAL NEST SURVIVAL

ABSTRACT

Among the strongest ecological correlates of nest predation rates is nesting habitat patch size. Across a diversity of ecosystems, patch size consistently shows a negative relationship with nest predation rates, but there remains considerable variation in the effect size. The area, shape, amount of edge, and quality of vegetation associated with a patch all correlate with patch size, and independently each can alter nest predation rates. Variation in animal behavior, both predator and prey, may explain much of the inconsistency we see in the nest predation patch size relationship; however, the picture is further complicated because the patch itself is not functioning in isolation. To understand how patch size affects nest predation, we attempted to tease apart the independent effects of patch size and ecological correlates using artificial nests with a full factorial design where treatments included small and large habitat patch sizes and low and high artificial nest densities. Then we incorporated treatments, measurements of vegetation structure surrounding nests, and habitat availability within the landscape into our survival analysis of 617 artificial nests across 12 study sites and two trials. We found that across our treatment groups the predicted daily survival rate of nests was similar, suggesting that the availability of additional nesting habitat in the landscape beyond fields directly bordering the nesting habitat diminished the effect of our patch size and nest density treatments creating a system where large and small patches have similar predicted nest survival.

INTRODUCTION

Nest predation has profound implications for avian systems, affecting the evolution and expression of life-history traits and reproductive behaviors (Thomas E.

Martin 1995, 1993), and shaping the ecology and conservation of breeding bird communities (Clark and Nudds 1991; Chalfoun, Thompson, and Ratnaswamy 2002). Given the importance of nest predation, it is not surprising that considerable attention is dedicated to understanding and explaining patterns of nest predation (Hartley and Hunter 1998; Chamberlain et al. 2009; Bender, Contreras, and Fahrig 1998). Among the strongest ecological correlates of nest predation rates is nesting habitat patch size, the area of suitable habitat patches available to a breeding bird population (Bender, Contreras, and Fahrig 1998; Winter and Faaborg 1999). Across a diversity of ecosystems, patch size consistently shows a negative relationship with nest predation rates (Johnson and Temple 1990; Hoover, Brittingham, and Goodrich 1995; Herkert 1994), but despite the consistency of the pattern, there remains considerable variation in the extent to which patch size explains nest predation rates in a given system (Winter et al. 2006; Clark and Nudds 1991).

The area, shape, amount of edge, and quality of vegetation associated with a patch all correlate with patch size (Hovel and Lipcius 2001; Davis 2004; Anderson, Cady, and Meikle 2003), and each can alter nest predation rates independently (Davis 2005; Lusk and Koper 2013; Angelstam 1986; Johnson and Temple 1990), most notably by altering predator search efficiency and thus nest encounter rates (Brown 1992; Barbosa and Castellanos 2005). Most nest predators are generalists that opportunistically consume nests when presented with the opportunity, but do not consistently search for or rely on nests in their diet (Vickery, Hunter, and Wells 1992; Lariviere and Messier 1997; Riley et al. 1998). As patch size increases, the area and complexity of the patch also increases, as well as the distance to alternative habitats that predators may otherwise occupy, all of which can reduce predator search efficiency (Angelstam 1986; Stephens et al. 2005). Faced with decreasing efficiency, generalist predators are likely to switch to alternative prey that require less effort (Schenk and Bacher 2002) leading to reduced nest predation rates in large patches. However, there is considerable variation in prey switching behavior, which reflects unique aspects of the environment (e.g., availability of other food resources; (Schenk and Bacher 2002)), and the predator (e.g., degree of specialization; (Murdoch 1969)).

Aspects of the patch clearly have direct implications to predator search efficiency, and thus nest predation rates, but birds also respond to patch characteristics and in doing so may indirectly affect predator search behaviors. Patch size can influence nest density by restricting birds to small patches at high densities, or by allowing birds to spread out across large patches at low densities. As nest density increases, encounter rates by opportunistic nest predators also increase, prompting a shift in foraging preference to nests and away from other food resources (Clark and Nudds 1991; Winter et al. 2006). Although the feedback mechanism from the predators perspective is similar (i.e., encounter rate), the relationship is further complicated because nesting density ultimately reflects the behavior of the bird. Interspecific variation in the willingness to tolerate conspecifics, or even heterospecifics with similar nest ecology, can create substantial differences in nest densities (Krebs 1971), and lead to the variation we see in nest predation rate even when patch sizes are similar.

Variation in animal behavior, both predator and prey, may explain much of the inconsistency we see in the nest predation patch size relationship; however, the question is further complicated because the patch itself is not functioning in isolation. It is increasingly apparent that ecological factors acting well beyond the borders of a patch affect populations dynamics (Stephens et al. 2003; Jorgensen et al. 2014), and nest predation rates in particular (Clark and Nudds 1991; Simonsen and Fontaine 2016). Landscapes with more suitable nesting habitat beyond the borders of the patch may support ecological conditions (e.g., lower generalist predator populations) that offset the costs of smaller patches per se, leading to situations where small and large patches have similar nest predation rates. To understand how patch size influences nest predation rates across systems, we need to isolate the mechanisms driving the inconsistent decrease in nest survival as patch size decreases.

We attempted to tease apart the independent effects of patch size from the often-correlated effects of nest density, vegetation quality within a patch, and habitat availability in the landscape to understand how patch size affects nest predation. We explored the interactions between patch size and environmental measures of predation risk by conducting a field experiment using artificial nests with a full factorial design where treatments included small and large habitat patch sizes and low and high artificial nest densities. We then incorporated treatments, measurements of vegetation structure surrounding nests, and habitat availability within the landscape into our survival analysis to understand the ecological conditions that ultimately drive patterns of nest predation risk.

METHODS

Study Area

The diverse land-use practices and topography of Furnas County, Nebraska provided an ideal mixture of grassland and cropland to study the influence of grassland patch size on nest predation rates. In areas with shallower slopes, corn and soybean fields predominated, along with additional dryland crops such as winter wheat and sorghum. In contrast, areas with rougher terrain were more likely to contain tracts of native mixed-grass pastureland.

Study Sites

We selected twelve grassland study sites representing two patch sizes, with six small patches ranging in size from 15-25 ha and six large patches ranging in size from 70-469 ha based on patches available. Within each of our large patches, we selected an area of 20 ha within which we subsequently conducted our experiment. Each patch, large and small, was randomly assigned one of two nest density treatments, low (one nest per every 2 hectares) or high (one nest per 0.5 hectare). We initiated our first trial in June 2016. After the completion of the first trial, the nest density treatment for each site was switched (e.g., from low to high), and we initiated a second trial in July 2016.

Artificial Nests

We chose to use artificial nests to examine the effects of patch size and nest density because artificial nests avoid biases associated with parental behaviors. Although artificial nests do not always adequately replicate real nests (Major and Kendal 1996; Moore and Robinson 2004), our study is focused on understanding the effects of ecological conditions on nest predation risk, and not parental behaviors. When careful assessment of methods and assumptions are considered, artificial nests can have value in examining environmental risk (Joseph J. Fontaine et al. 2007). The predation risk that real nests experience varies with nest site selection and parental behaviors, potentially confounding the risk associated with a particular environment (Joseph J. Fontaine et al.

2007). By creating artificial nests that mimicked real nests in appearance, substrate, and egg characteristics, but possess consistent nest coverage and no variation in parental behaviors, we were able to assess differences between the inherent risk associated with patch size and nest density. We expect that any biases associated with using artificial nests are consistent across study sites, and variation in density effects between study sites are accounted for by switching density treatments between trials. Therefore, differences we find in nest success rates do not reflect differences in real nest survival rates, but instead represent variation in the inherent risk associated with patch size and nest density.

We used artificial Northern bobwhite (*Colinus virginianus;* hereafter bobwhite) nests to examine how predation risk varied across different patch sizes and different nest densities. For each trial, we created a random grid over the patch using QGIS with the number of required nest points based on the assigned nest density treatment (QGIS Development Team, 2017, QGIS Geographic Information System. Open Source Geospatial Foundation Project: http://qgis.osgeo.org). We mimicked bobwhite nests by placing three bobwhite eggs in a canopied nest similar in appearance to bobwhite nests observed within the study area. First, we found the location of the nest point using a Garmin eTrex 10 Geospatial Positioning System (Garmin Ltd.). We then selected a clump of warm season grass with a surrounding litter depth of 3 cm for our nest location to ensure consistency in the appearance of the nest, and created a nest canopy by forming a small opening and chamber within the vegetation and litter, with the nest opening facing south. We constructed a nest bowl using vegetation cut from the surrounding area, and completed the nest by placing three bobwhite eggs in the nest bowl, which we then placed underneath the nest canopy. To reduce the influence of nest cover on nest success, we consistently hid eggs so less than 20 percent of the nest was visible through the nest opening from one meter away.

Each trial lasted 23 days to imitate the incubation period of the bobwhite (Klimstra and Roseberry 1975). We checked nests every four days, and considered a nest successful if all eggs remained intact for the entire 23-day trial. To identify nest predators, we randomly monitored four nests within each site with a trail camera (Moultrie M-880, Moultrie, EBSCO Industries, Inc.) placed 0.5m south of the nest, set 15 cm above the ground, and programed to take three pictures when movement was detected.

To understand how density and patch size influenced nest survival rates, we fitted a mixed-effect model in a Bayesian framework to model survival using MCMC simulations in JAGS (Plummer 2003) with the package R2jags (Su and Yajima 2015) in R (R version 3.4.3, R Core Development Team 2016). Nests experience predictable seasonal decline in success (Fields et al. 2006; Decker, Conway, and Fontaine 2012); therefore, we examined the interaction between patch size, nest density, and trial to account for temporal variation in nest success between nest density treatments in each patch size during different trials. To incorporate the temporal interaction, we included all combinations of trial, patch size, and nest density as separate intercepts, resulting in eight unique treatment variables that were estimated (e.g., the groups small patch/high density/trial 1, and large patch/high density/trial 1 both had estimated intercepts).

Local Nest Conditions

To understand how vegetation surrounding each nest site influences nest success, we conducted a vegetation survey according to BBIRD Field Protocol (T. E. Martin et al.

1997) at each nest after either the nest was depredated or the trial concluded. We measured the maximum vegetation height and estimated nest concealment from four cardinal directions at a distance of one meter and directly above the nest. We also measured maximum vegetation height, and visually estimated the percent cover of warm season grasses, cool season grasses, forbs, shrubs (diameter less than 1.5 cm), trees (diameter greater than 1.5 cm), litter, and bare ground within a five-meter radius of the nest.

We examined the effects of local vegetation by incorporating vegetation structure into our Bayesian model, including vegetation height within 5m, and proportion of cool season grasses, forbs, litter, and bare ground. We did not include warm season grass because of the high correlation with cool season grass (r = -0.7), and the greater variation in the of cool season grass among samples. Shrubs and trees were absent from the majority of the nest sites, so we did not use the proportion of shrubs or the proportion of trees in our model.

Landscape Conditions

The amount of habitat available within the larger landscape the ecological neighborhood plays an important role in shaping population dynamics (Jorgensen et al. 2014) including nest success (Simonsen and Fontaine 2016). To understand how the ecological neighborhood may influence success of our artificial nests, we digitized land use within a 2 km radius buffer for each of our twelve sites using QGIS (QGIS Development Team, 2017 QGIS Geographic Information System. Open Source Geospatial Foundation Project: http://qgis.osgeo.org). Land use categories included grassland, row crop, small grains, trees, and fallow; however, because crop and small grains were correlated with grassland (r = -0.5 and -0.5 respectively) we used the total area (ha) of grassland and total distance of edge (km) within the digitized 2km buffer.

We recorded the shapefiles and rasterized each in R (R Core Development Team 2016) using the package raster (Hijmans and van Etten 2012). We used the raster files to calculate the total area (ha) dedicated to each land use class, as well as the total distance of edge (m) between classes within a 0.5, 1, 1.5, and 2 km buffer radius using the package spatialEco (Evans 2017). Measuring land use and edge distance at the four selected scales allowed us to determine if the land use in the immediate surroundings of a field (indicating the importance of patch size and the habitat directly adjacent), or the larger landscape (indicating the importance of additional habitat in the landscape) had a greater influence over nest survival.

We used Bayesian latent indicator scale selection (hereafter BLISS, Stuber, Gruber, and Fontaine 2017) to determine the spatial scales where grassland area and total edge distance could best explain nest survival from candidate spatial scales with buffer radii of 0.5, 1, 1.5, or 2 km. At each iteration of the reversible-jump MCMC sampling procedure, BLISS independently selects a candidate scale for grassland area and edge distance, concurrently sampling a coefficient for each variable as well as other predictors not undergoing spatial scale selection. As the model moves through iterations, candidate spatial scales are sampled in proportion to their posterior probability. Therefore, after the completion of all iterations, in addition to having posterior probability distributions of model coefficients, we also have posterior distributions for the spatial scales for the amount of grassland and edge length. We ran the BLISS analysis 10 times to quantify variation in scale selection by comparing the distributions, mean and credible intervals, and rank order of posterior probability for each scale. We then selected the best scale with the highest explanatory power based on the highest posterior probability distribution, highest mean posterior probability without overlapping credible intervals with other scales, and lowest average rank. If all three comparisons selected a single scale, we concluded that support for that scale was strong.

After selecting the most informative spatial scale for each landscape variable, we ran our mixed effects model with eight treatment intercepts, local vegetation characteristics, landscape variables at their selected scales, and included study site as a random effect to account for variation between sites. We scaled and centered continuous covariates (i.e., local vegetation and landscape variables) so that the variables had comparable units. We modeled daily survival of individual i, ϕ_{it}, as a series of Bernoulli trials formulated as:

$$logit(\phi_{it}) = T_1 * \beta_{T1} + \dots + T_1 * \beta_{T1grassland} * (grassland\ area)_i + \dots + (edge\ distance)_i * \beta_{edge\ distance} + (vegetation\ height)_i * \beta_{vegetation\ height} + (cool\ season\ grass)_i * \beta_{cool\ grass} + (forbs)_i * \beta_{forbs} + (litter)_i * \beta_{litter} + (bare\ ground)_i * \beta_{bare\ ground} + site_i$$

Where T represented our treatment dummy variable, β was a vector of coefficients associated with each of our covariates, and $site$ was a random effect. We present results based on 200,000 MCMC samples of model parameters after 1,000 iterations of burn-in. We visually inspected trace plots to confirm convergence.

We examined the relationship between each predictor variable and nest survival rates by predicting daily survival rates for each treatment group separately across the range of scaled and centered values for each predictor. Because the amount of grassland area was hypothesized to be an important predictor of nest survival, and because grassland area systematically differed between the patch size treatment groups, for our visualizations we hold site-specific grassland area at the patch size treatment group means. All other variables were held at the grand-mean. After back transforming the predicted daily survival rates for each treatment, we then averaged the mean across treatment groups to create a single prediction curve. Once predicted responses were calculated, our predictor variables were de-centered and de-scaled to examine the relationship across the actual values of our predictor. Furthermore, we examined the predicted nest survival rate by taking our predicted daily survival rate to the 23rd power (i.e., the average incubation period for bobwhites; Klimstra and Roseberry 1975).

RESULTS

We monitored 617 artificial bobwhite nests, 314 during trial 1 and 303 during trial 2. A total of 329 nests survived the two 23-day trial (incubation) periods, resulting in 53% survival including 61.4% in small patches, 45.8% in large patches, 56.1% in high density patches, and 42.4% in low density patches. Nest predators recorded at the randomly assigned artificial nests included coyotes (*Canis latrans*, 1), raccoons (*Procyon lotor*, *3*), American badgers (*Taxidea taxus*, *1*), striped skunks (*Mephitis mephitis*, *8*), opossum (*Didelphis virginiana*, 1), and small rodents (e.g., *Ictidomys tridecemlineatus,* 5).

The influence of our eight treatment groups varied widely for small patch size treatment groups, whereas large patch size treatment groups were consistent. Overall, the treatment groups associated with large patch sizes (e.g., low density/large patch/trial 1) had credible intervals that did not overlap zero, indicating strong positive effects of treatment on nest survival (Figure 1.1). Half of the small patch size treatment groups (i.e., low density/small patch/trial 1 and high density/small patch/trial 2) also indicated strong positive effects of treatment on nest survival with credible intervals that did not overlap zero. In contrast, the remaining groups (i.e., high density/small patch/trial 1 and low density/small patch/trial 2) possessed credible intervals that overlapped zero and indicated weak positive effects of the treatment on nest survival.

The strength of effect for local vegetation also varied. The average proportions of cool season grass and litter both had strong effects on nest survival (negative and positive, respectively; Figure 1.2). The credible intervals of the average proportion of forb cover estimate crossed zero, but the mean estimate is farther from zero indicating a weak positive effect. The average proportion of bare ground and average height of vegetation possessed credible intervals that cross zero and mean estimates near zero, also indicating no effects on nest survival.

The BLISS analysis indicated that the area of grassland and total edge-distance were both most informative at the 0.5 km radius scale. For grassland area, the 0.5 km radius buffer scale was selected because the 0.5 km scale probability ranged from 0.81 to 0.89, possessed a mean of 0.85 (±0.01 credible interval), and was ranked first in each iteration. For total edge distance, the 0.5 km radius buffer scale probability ranged from 0.3 to 0.32, possessed a mean of 0.31 (±0.003 credible interval), and was ranked first in each iteration. The percent of the 0.5km radius buffer designated as grassland ranged from 54.6% to 96.7% for large patch sites and 30.0% to 52.9% for small patch sites, with a mean of 69.3% and 42.3%, respectively. In contrast, the total edge distance within the

0.5km radius buffer ranged from 7.19km to 15.5km and 11.5km to 23.5km for large and small patch sites, respectively.

When we predict the daily survival rate of artificial nests in each of our treatment groups, we find similar survival rates across all groups because all treatment groups possessed a positive effect (Figure 1.3). Differences between treatments in the second trial are greater than the first trial, but are not likely to be important because the credible intervals overlap. Mean predicted nest survival rates varied more between treatments, but the credible intervals overlap almost entirely indicating that we cannot distinguish distinct differences in artificial nest survival between treatments.

DISCUSSION

The selection of the 0.5km radius buffer by BLISS indicates that it is important to account for variation in land use immediately surrounding nesting habitat patches. In our study system, small patches varied in the amount of isolation from other grassland patches, and large patches of nesting habitat were not completely isolated from cropland patches. Therefore, outside of the dichotomy of small and large patches, variation in the isolation of small patches and the separation of large patches from cropland influenced nest survival. However, all the treatment groups possessed a positive effect on artificial nest survival, so when we examine predicted survival our treatment groups all have similar predicted survival. The lack of differences in survival between the large and small patches in our study, when variation in the amount of grassland in the local landscape is accounted for, indicates either an alternative mechanism is creating conditions where the effects of nesting habitat patch size does not influence inherent nest predation risk, or the availability of grassland habitat in the larger landscape masked the effects of patch size.

We found variation in the abundance of grassland on the landscape between small and large patch study sites at the 0.5 km radius buffer (30.0% to 52.9% and 54.6% to 96.7%, respectively, Figure 1.5). However, the amount of grassland within the landscape at the 2km radius buffer was similar between small and large patch study sites (32.7% to 63.3% and 37.5% to 61.1%, respectively, Figure 1.5). As a result, despite the amount of habitat available within close proximity to the study sites, additional grassland habitat was present around each site in the larger landscape. The availability of additional foraging habitat for opportunistic nest predators may have spread the foraging focus of predators across the landscape more evenly, rather than concentrating predator foraging focus on a few patches of habitat. When predator foraging focus is more evenly spread across the landscape, and predator populations do not show a numeric response to prey abundance, then small patches may experience greater survival in landscapes with additional habitat when compared to small patches in landscapes with very little additional habitat present (Phillips et al. 2003; Stephens et al. 2005; Clark and Shutler 1999). Predators may be less likely to come across isolated small patches compared to large patches, potentially offsetting the efficiency of predators when they do find small patches (Cody 1971; Seymour, Harris, and White 2004). Alternatively, predators may focus on larger patches of habitat that are more likely to provide all the resources required for subsistence and continual support for predator communities (MacArthur and Pianka 1966; Ford 1983).

The lack of distinct differences between our treatment groups adds testament to the long line of studies that found that a complexity of mechanisms driving patch size effects on nest survival (Winter et al. 2006; Clark and Nudds 1991). Although our results were unexpected, we are confident in our results because of our robust sample sizes, rigorous experimental design, and thorough analysis that incorporated the environmental conditions often correlated with patch size. We also are confident that the artificial nests we created served as adequate surrogates for real nests based on survival rates and the observation of nest predators similar to real nests (Taylor, Church, and Rusch 1999; Klimstra and Roseberry 1975). In addition to similarities in nest predators, the relationships we found between local vegetation characteristics and nest survival align with the findings of previous research with natural nests where increases in vegetation structure and cover result in increased nest survival (Davis 2005; Lusk and Koper 2013). For example, an increase in the proportion of litter indicates an increase in vegetation cover, which leads to an increase in nest survival (Figure 1.4a). Conversely, as the proportion of cool season grasses increase, and thus warm season grasses decrease, cover decreases and nest survival decreases (Figure 1.4b).

Identifying optimal locations to prioritize the conservation of breeding populations of grassland birds requires teasing apart the separate influences of nest density, patch size, habitat availability within the landscape, and local vegetation on nest predation risk. Separating the pieces influencing nest predation risk and examining each individually may allow us to identify the biological and opportunity costs associated with conservation in patchy landscapes. After controlling nest density, carefully selecting sites with small and large patch sizes, accounting for the habitat availability within the 0.5km radius buffer area around our study sites, and incorporating the effects of vegetation surrounding each artificial nest, we found no effect of patch size on inherent nest predation risk within our study system. When small patches of nesting habitat are situated in landscapes that provide additional predator foraging habitat, the addition of a small habitat patch may provide nesting opportunities with similar success rates as large patches. Additional research examining how the abundance of grassland within the local landscape, as well as the larger landscape, would allow us to estimate the amount of grassland within a larger landscape that is required to offset the effects of elevated risk associated with small nesting habitat patches is needed. However, from this research, we can conclude that examining the larger landscape before selecting patches for habitat restoration is important in determining whether small or large patches will provide the greatest opportunities for nest and conservation success.

TABLES AND FIGURES

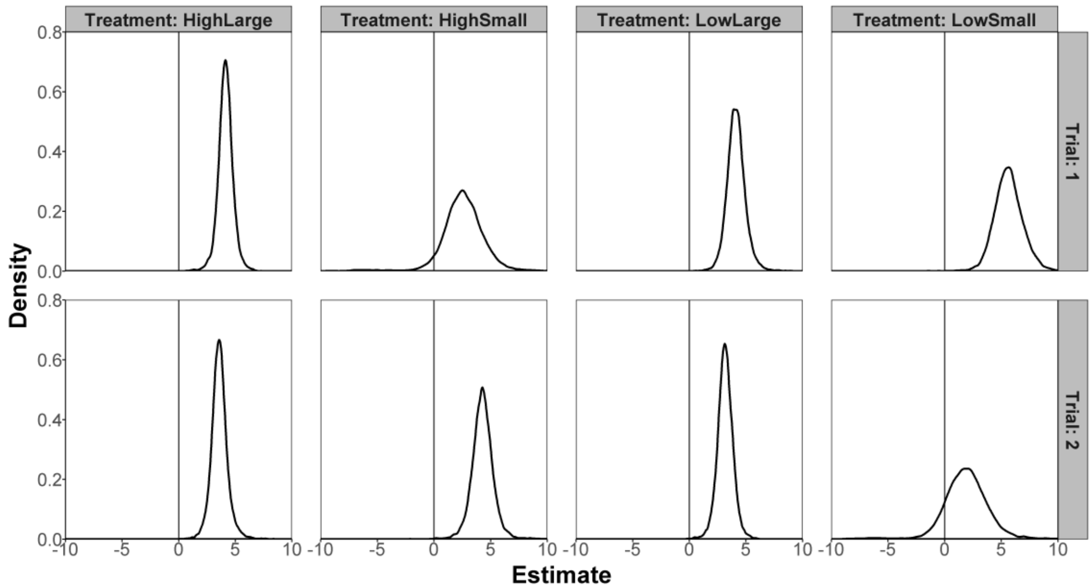

Figure 2. 21 Density plots of credible intervals for estimates for each treatment group indicate that treatment groups associated with large patches all had strong positive effects on nest survival, but the strength of the positive effect varied across treatment groups with small patch size.

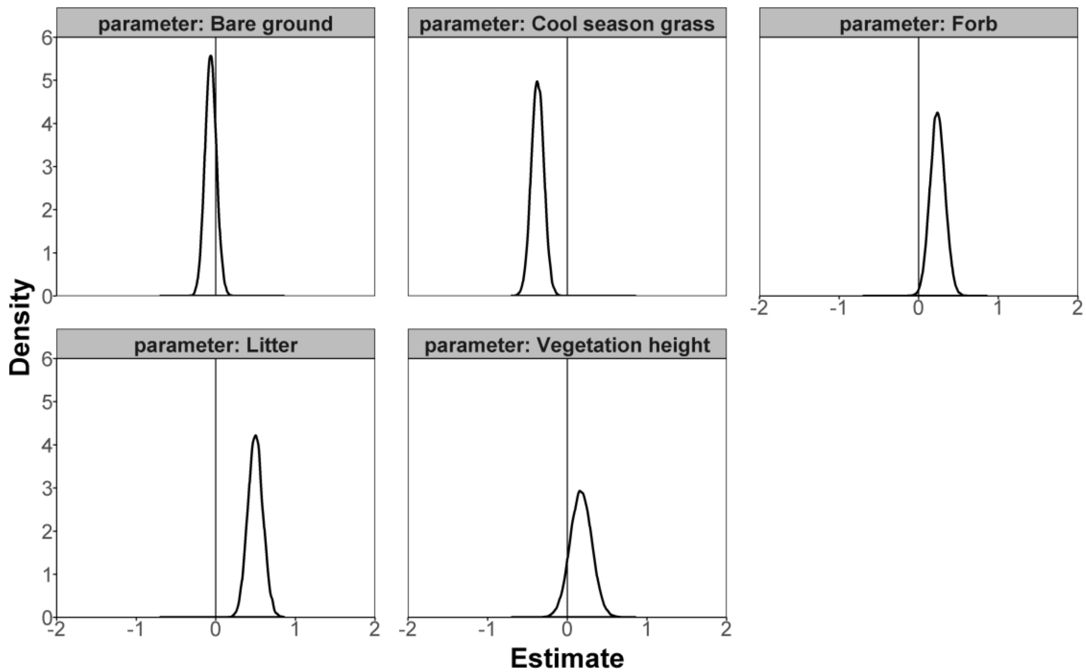

Figure 2. 22 The average proportions of cool season grass and litter have strong effects on nest survival (negative and positive, respectively), whereas the average proportion of forbs possesses a weak positive effect based on posterior distributions that cross zero. The average proportion of bare ground and average vegetation height have very weak effects on nest survival due to posterior distributions that greatly overlap zero.

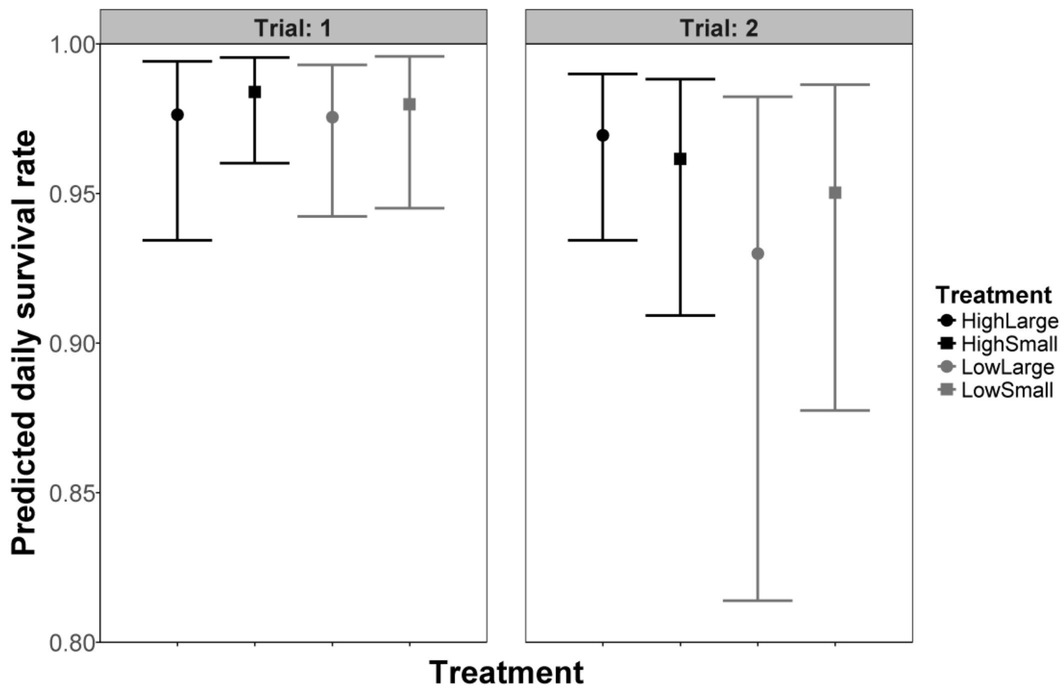

Figure 2. 23 Predicted daily survival rates were similar across all treatment groups. Greater differences are exhibited in second trial, but the credible intervals overlap almost entirely indicating that we cannot distinguish distinct differences in artificial nest survival between treatments

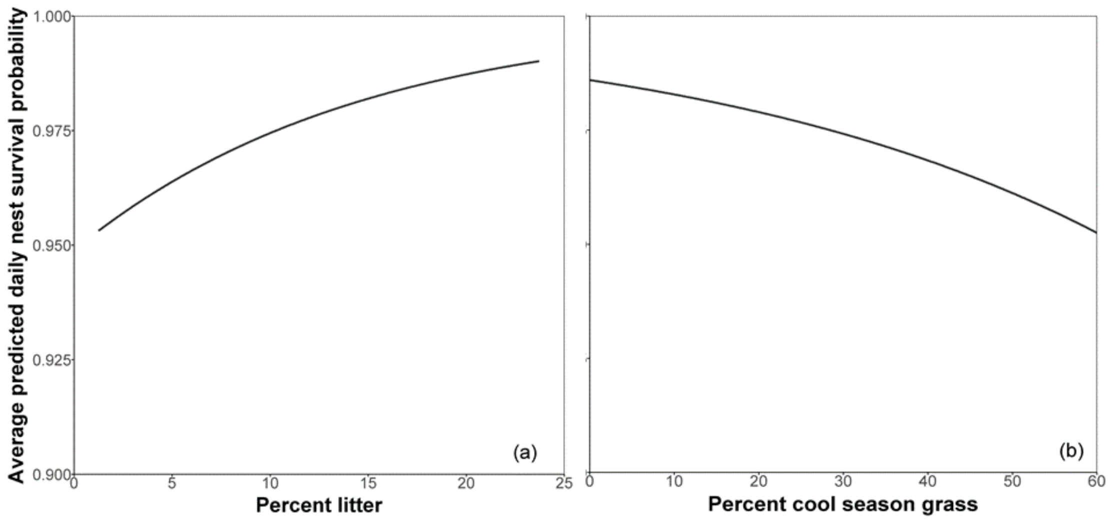

Figure 2. 24 Predicted daily survival rates were positively related to the percent litter (a) and negatively related to the percent cool season grass (b) in the 5m radius surrounding artificial nests.

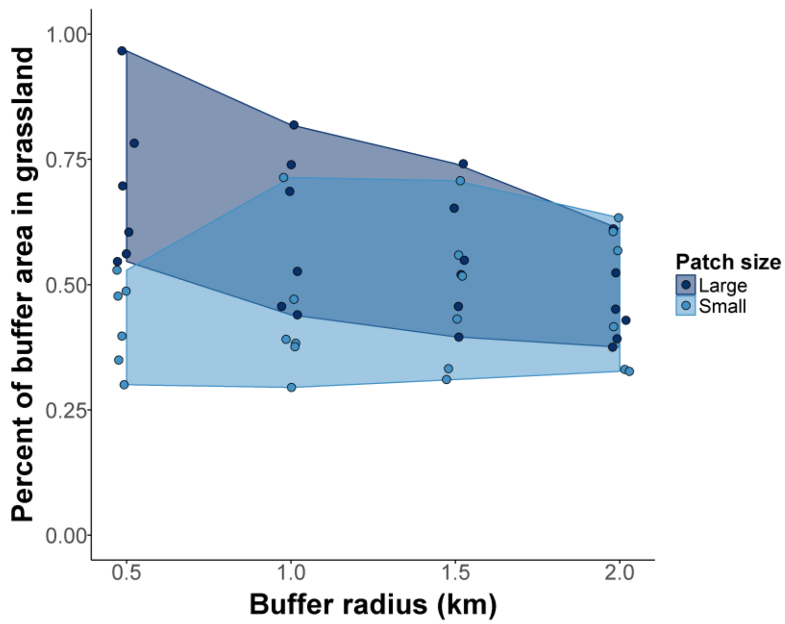

Figure 2. 25 The percent of grassland within the total buffer area had a wider range at the 0.5 than the 2 km buffer radius.

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APPENDIX A

The following are guidelines used to sort articles by Media Type, Article Type, and Experiment Type for analyses.

1. ***Media Type***: what type of publication the article is
    a. Journal Article: an article that has been peer reviewed and published in a scientific journal, also included conference papers
    b. Book: a whole book or excerpt/chapter from a book
    c. Report: a report to or from a government agency (not peer reviewed)
    d. Thesis: an unpublished master's or doctoral thesis

2. ***Article Type***: what type of information is presented in the article:
    a. Comment: the article talks about artificial nests (i.e., discusses results from an article with artificial nests, mentions artificial nest use, etc.)
    b. Experiment: article is about an experiment where artificial nests are used directly in the experiment
    c. Meta-analysis: compilation of results from multiple studies that are used in a new analysis
    d. Not relevant: article is not about artificial nests or uses artificial nests in ways outside of the focus of the meta-analysis (i.e., artificial nests of non-avian species, chick/brood rearing only, artificial nests used in laboratory tests, artificial nest structures built by people for birds to use, artificial nests that lack real or fake eggs as bait, etc.)
    e. Review: article is an extensive review of literature without compiling results for meta-analysis

3. ***Experiment Type***: what type of experiment was conducted
    a. Artificial only: only artificial nests were used in the experiment (comparisons to real nest data from studies over 5 years prior, different researchers, and/or different areas are not applicable)
    b. Artificial and real: artificial and real nests were used in the experiment (or by the same researcher teams in the same area at approximately the same time)

APPENDIX B

The following are information collected from each article as background information about the studies to assist with analysis.

1. ***Pub_ID:*** Row specific identification key to identify specific treatments from studies based on the last name of first author; year of publication; publication number by the specified author in specified year; letter indicating which study from article (some articles include multiple questions, nest types, nest placements, and/or species that were separated into different studies when data for each study was available); and letter indicating which treatment the row of data represents, all separated underscores (e.g., ACKERMAN_2004_1A_A is the first treatment from the first study in the first article published by Ackerman in 2004).
2. ***Pub_ID2:*** A shortened version of the Pub_ID meant to distinguish individual studies based on last name of first author, year of publication, publication number, and study identifier separated by underscores (e.g., ACKERMAN_2004_1A).
3. ***Pub_ID3:*** Article identification key based on last name of first author, year of publication, and publication number by specified author in specified year separated by underscores (e.g., ACKERMAN_2004_1).
4. ***Authors:*** Authors of the article.
5. ***Article_title:*** Title of the article.
6. ***Publication_year***: Year the article was published.
7. ***Journal_title:*** Title of the peer-reviewed journal the article was published in.
8. ***Start_year:*** Year that data collection began.
9. ***End_year:*** Year that data collection ended.
10. ***Study_length:*** end_year minus start_year
11. ***Country:*** Country where the research was conducted. *(note: Antarctica was included as a country)*
12. ***State:*** State within the United States where the research was conducted.
13. ***Longitude:*** Longitude where the research was conducted.
14. ***Latitude:*** Latitude where the research was conducted.
15. ***Abs_latitude:*** Absolute latitude where the research was conducted.
16. ***Habitat_type:*** type of habitats where research was conducted.
    a. Agricultural: cropland dominated ecosystem
    b. Grassland: a grass and forb dominated habitat
    c. Forest: a tree dominated ecosystem
    d. Urban: human structure dominated habitat
    e. Wetland: a habitat dominated by hydric soils, water loving plants, and water

APPENDIX C

The following variables are information collected on the methods used in the articles studied to account for variation associated with study systems and methods in the meta-analysis.

1. ***Order:*** Phylogenetic order the study species belonged to.
2. ***Family:*** Phylogenetic family the study species belonged to.
3. ***Species:*** Species studied whose nest survival was compared to artificial nest survival.
4. ***Nest_type:*** The structural nest type of the artificial nests.
    a. Burrow: very effective at protecting eggs and young from predators and maintaining an appropriate microclimate for eggs and young. Some birds, like Bank Swallows and Belted Kingfishers, usually construct their own burrows, while others, such as Burrowing Owls, may use the burrows constructed by other species.
    b. Cavity: used by numerous passerines, woodpeckers, owls, parrots, and some waterfowl.
    c. Closed cup: cup shaped nest with a canopy that covers the nest
    d. Open cup: cup shaped nest with an open top
    e. Platform: are relatively flat nests that may be located on the ground, in a tree, or on the tops of rooted vegetation or debris in shallow water.
    f. Primary cavity: construct their own cavity nests.
    g. Scrape: simple depressions in the ground (sometimes with a few stones or leaves added), or in the leaf litter. Such nests are used by shorebirds, gulls, terns, nighthawks, vultures, and other species.
    h. Secondary cavity: species that use natural cavities or cavities constructed by primary cavity nesters.
5. ***Nest_type_similar:*** The type of artificial nest used was similar (yes) or different (no) to the nest type used by the species being mimicked.
6. ***Nest_construction:*** Artificial nest construction by research was grouped into six categories, including:
    a. Artificial structure appropriate: constructed by researchers out of appropriate materials
    b. Artificial structure not appropriate: constructed by researchers out of inappropriate materials or poorly mimics the target species nest
    c. Depression: a simple depression in the ground was used to simulate scrapes that lacked any vegetation lining
    d. No nest: no nest was used, eggs/bait were placed directly on the ground
    e. Real different species: real nest from a species other than the target species was used
    f. Real target species: real nests from the target species were used
7. ***Nest_placement:*** At what height was the artificial nest placed:
    a. Ground: nest is placed on the ground
    b. Shrub: nest is placed above ground to 3 meter off the ground
    c. Canopy: nest is place 3 meters or more above ground

8. ***Nest_placement_similar:*** The placement of the artificial nests was similar (yes) or different (no) from the placement of real nests
9. ***Nest_height:*** The average height artificial nests were placed at in m.
10. ***Egg:*** The species and/or materials used to make eggs placed as bait in the artificial nests:
    a. Ceramic: clay hardened by heat in the shape of a bird egg
    b. Clay: modeling clay that is left unhardened (to show impressions from predators) shaped to resemble a bird egg
    c. Wax: any of various substances resembling the wax of bees in the shape of a bird egg
    d. Plasticine: a plastic modelling paste shaped to resemble a bird egg
    e. Chicken: any type of chicken egg
    f. Pheasant: egg from any species of pheasant
    g. Quail: egg from any species of quail
    h. Budgie: egg from any species of budgie
    i. Finch: egg from any species of finch
    j. Sparrow: egg from any species of sparrow
11. ***Eggs_used:*** the type of eggs used as bait in the artificial nests:
    a. Artificial: only artificial eggs made from clay or wax
    b. Artificial and real: both artificial and real eggs were placed in nests
    c. Real: only real eggs were used as bait
12. ***Egg_width:*** The width of real eggs in mm.
13. ***Egg_length:*** The length of real egg in mm.
14. ***Egg_volume:*** The volume of a real egg calculated by 0.507 * (egg_length*((egg_width)^2))/1000 in ml based on (Hoyt 1979)
15. ***Artificial_egg_width:*** The width of artificial eggs in mm.
16. ***Artificial_egg_length:*** The length of artificial eggs in mm.
17. ***Artificial_egg_volume:*** The volume of the artificial egg calculated by 0.507 * (egg_length*((egg_width)^2))/1000 in ml based on (Hoyt 1979)
18. ***Body_mass:*** The average adult body mass in g.
19. ***Real_clutch_size:*** The number of eggs in real clutches.
20. ***Artificial_clutch_size:*** The number of eggs in artificial clutches.
21. ***Clutch_diff:*** The artificial clutch size – real clutch size.
22. ***Reproductive_Investment:*** A measure of investment in reproduction based on adult body mass (g) / (real clutch size * egg volume) (ml)
23. ***Incubation_days:*** The average number of days real eggs are incubated before hatching.
24. ***Exposure_days:*** The number of days artificial eggs were exposed.
25. ***Real_visitation:*** The number visitations to real nests.
26. ***Artificial_visitation:*** The number of visitations to artificial nests.
27. ***Visit_diff:*** The number of artificial nest visits – the number of real nest visits.

APPENDIX D

The following are information collected from articles on results used to analyze survival and explore patterns across specific questions/treatments.

1. ***Question_Category:*** The type of question studied by the treatments that survival results were reported for.
   a. Landscape characteristics: Questions focused at the landscape scale and beyond the boundaries of the habitat patch.
   b. Local habitat characteristics: Questions focused on aspects of the habitat within the patch.
   c. Methodology: Questions focused on methods used by the investigators.
   d. Nest characteristics: Questions focused on the features and appearances of nests.
   e. Predators: Questions focused on predator communities, behaviors, and efficacy of control efforts.
   f. Real vs artificial: Questions focused on the difference in survival of real and artificial nests.
2. ***Treatments***: The type of treatments used in the study to address questions, we attempted to divide each of the treatments groups within the question category into two treatments for comparisons across studies unless treatments were not of concern:
   note: other treatments were treatments used in only one article
   a. Landscape characteristics:
      i. Fragmentation: high and low fragmentation in the landscape
      ii. Island vs mainland: isolated island and connected mainland habitat patches
      iii. Patch size: small and large habitat patches in the landscape
      iv. Other treatments: surrounding habitat
   b. Local habitat characteristics:
      i. Colonial vs solitary: nests within colonies and nest outside colonies in solitary
      ii. Distance to edge: nests near and far from edges or edge habitat
      iii. Habitat: the type of habitat in the patch
      iv. Microhabitat: the habitat conditions directly surrounding the nest
      v. Neighbor effects: the effect of neighboring nests from the same and/or different species
      vi. Nest density: high and low densities of nests in the area surrounding nests
      vii. Vegetation density: high and low vegetation cover/structure surrounding nests
      viii. Year: the year of data collection, used when there were multiple years of data collection and no clear treatment to assign
      ix. Other treatments: edge composition, habitat quality, invasive species removal, trial
   c. Methodology:

- ***i.*** Nest camera: whether a nest camera was or was not placed at the nest site
- ***ii.*** Other treatments: nest check, visitation rate

d. Nest characteristics:
- ***i.*** Breeding season: whether nests were placed early or late in the breeding season
- ***ii.*** Egg size: small and large eggs in the nests
- ***iii.*** Egg type: what egg was used as bait in the artificial nests, primarily focused on species
- ***iv.*** Nest cover: high and low nest concealment
- ***v.*** Nest Guild: the type of nest
- ***vi.*** Nest Placement: whether the nest was placed on the ground, in a shrub, or in a tree
- ***vii.*** Nest substrate: the material used to construct the nest or incorporated into the nest structure
- ***viii.*** Real vs artificial: whether real or artificial eggs were used in the artificial nests as bait
- ***ix.*** Other treatments: clutch size, decoy nest, moon illumination, nest height, nest materials, nest size, nest type, stone rampart, study site, trial

e. Predators:
- ***i.*** Predator removal: predators removed and not removed from sites
- ***ii.*** Predator repellents: predator repelling scents placed around the nest and not placed around the nest
- ***iii.*** What predators: treatments divided up based on what predators predated nests and/or the main objective was to only determine what predators predated real and/or artificial nests
- ***iv.*** Other treatments: predator activity, predator exclusion, predator repellents

f. Real vs artificial:
- ***i.*** Real vs artificial: main objective was to determine differences in survival between real and artificial nests, no treatments assigned
- ***ii.*** Other treatments: study site

3. ***Real_Treatments:*** The treatments associated with the real nests.
   a. None: no treatments were assigned
   b. Not separated: survival results from treatments were not separated
   c. Question and treatment group based treatments
4. ***Real_T:*** How the real nest data is to be recorded based upon treatments.
   a. Single: include the real nest data as a separate line of data
   b. Average: include the real nest data as an average across all rows associated with the study
   c. Include: only include the real nest data from this treatment from this study
   d. Exclude: do not include the real nest data from this treatment from this study
   e. Repeat: do not include the real nest data from this treatment because it has already been included under another treatment (if there is more than one treatment for artificial nests, but no treatments for real nests)

5. ***Artificial_Treatments:***
    a. None: no treatments were assigned
    b. Not separated: survival results from treatments were not separated
    c. Question and treatment group based treatments
6. ***Artificial_T:***
    a. Single: include the artificial nest data as a separate line of data
    b. Average: include the artificial nest data as an average across all rows associated with the study
    c. Include: only include the artificial nest data from this treatment from this study
    d. Exclude: do not include the artificial nest data from this treatment from this study
    e. Repeat: do not include the artificial nest data from this treatment because it has already been included under another treatment (if there is more than one treatment for real nests, but no treatments for artificial nests)
7. ***Survival_measure:*** When success of real nests was measured:
    a. Fledged: a nest was successful when at least one nestling fledged
    b. Hatched: a nest was successful when at least one egg hatched
    c. Unknown: nest success measure was not clearly stated
    d. Others as specified by articles (e.g., 3 days, 4 days, third day of incubation, etc.)
8. ***Real_survival:*** How many of the eggs (or nestlings) had to succeed for the nest to be a success.
    a. 1: only one egg (or nestling) had to survive
    b. All: all eggs (or nestlings) had to survive
    c. Single: the clutch was made up of a single egg (or nestling)
    d. Unknown: could not determine based upon information in the article
9. ***Artificial_survival:*** How many of the eggs had to succeed for the nest to be a success.
    a. 1: only one egg had to survive
    b. All: all eggs had to survive
    c. Single: the clutch was made up of a single egg
    d. Unknown: could not determine based upon information in the article
10. ***Valid:*** Whether or not the study used appropriate methods and data are appropriate to compare (e.g., nests in areas baited with fish to draw predators in are not valid)
11. ***Colony:*** Whether or not the study was based on colonial nests, for overall analyses colonial nests were excluded to avoid excess variation.
12. ***Real_sample:*** The number of real nests.
13. ***Artificial_sample:*** The number of artificial nests.
14. ***Real_num_survived:*** The number of real nests that survived (for studies that reported nest survival rate this is the real nest survival rate * real sample).
15. ***Artificial_num_survived:*** The number of artificial nests that survived (for studies that reported nest survival rate this is the artificial nest survival rate * artificial sample).
16. ***Real_num_failed:*** The real_sample – real_num_survived.

17. ***Artificial_num_failed:*** The artificial_sample – artificial_num_survived.
18. ***ANS_real:*** Apparent nest success of real nests, the real_num_survived/real_sample (for studies that reported nest survival rate this is the real nest survival rate).
19. ***ANS_artificial:*** Apparent nest success of artificial nests, the artificial_num_survived/artificial_sample (for studies that reported nest survival rate this is the artificial nest survival rate).
20. ***DSR_real:*** Daily survival rate of real nests, the predicted probability of a nest surviving a single day.
21. ***DSR_artificial:*** Daily survival rate of artificial nests, the predicted probability of a nest surviving a single day.
22. ***NSR_real:*** Nest survival rate of real nests calculated by converting daily survival rate using the equation: daily survival rate ^ number of incubation days
23. ***NSR_artificial:*** Nest survival rate of artificial nests calculated by converting daily survival rate using the equation: daily survival rate ^ number of incubation days

APPENDIX E

The following are covariates incorporated into the generalized linear mixed effect models that were used to test patterns in nest survival based upon theories.

1. ***Survival:*** The nest survival rate and apparent nest success for both real and artificial nests
2. ***Sample:*** The total number of nests
3. ***Nest:*** Whether the data was from real or artificial nests
4. ***Exposure_days:*** The incubation days from real nests and exposure days from artificial nests
5. ***Abs_latitude:*** the absolute value of the latitude that the study was conducted at
6. ***Habitat:*** The type of habitat the study was conducted in
7. ***Nest_type:*** The structural nest type of the nests
8. ***Nest_placement:*** At what height the artificial nest was placed
9. ***Nest_size:*** The total volume of the clutch (egg volume * clutch size)
10. ***Visitation:*** The number of times investigators visited nests
11. ***Pub_ID:*** Row specific identification key to identify specific treatments from studies based on the last name of first author; year of publication; publication number by the specified author in specified year; letter indicating which study from article (some articles include multiple questions, nest types, nest placements, and/or species that were separated into different studies when data for each study was available); and letter indicating which treatment the row of data represents, all separated underscores (e.g., ACKERMAN_2004_1A_A is the first treatment from the first study in the first article published by Ackerman in 2004).