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RESEARCH ARTICLE

Nest architecture, not egg type, influences artificial nest survival in Brazilian coastal shrubland

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ABSTRACT. Experiments with artificial nests are widely used to gain insights into the behavioral and ecological factors affecting the survival of natural nests. Undesired effects on nest success may arise from variations in nest and egg characteristics (e.g., dimensions, texture, and color). Still, evaluating these potential factors is seldom considered in the design of artificial nest studies, particularly in tropical regions. We assessed the effect of two nest types (cup-shaped and dome-shaped) and two egg types (differing in size and color) on the survival of artificial nests. The egg types included smaller (22–25 mm), variously colored eggs of blue-breasted quails, *Synoicus chinensis* (Linnaeus, 1766) and larger (25–30 mm), white-spotted-with-brown eggs of Japanese quails, *Coturnix japonica* Temminck & Schlegel, 1848. The experiment took place within a coastal shrubland (restinga) in southeastern Brazil, from August 16–31, 2017. This period coincides with the onset of the breeding season for most insectivorous bird species in the region. The nests were observed for 15 days to assess predation, revealing higher survival rates in dome-shaped nests than cup-shaped ones. Egg type, however, did not affect survival rates. This suggests that coastal shrubland nest survival is influenced by factors seen in other Neotropical environments, where dome-shaped nests are likewise less vulnerable to predation. Interestingly, egg color and size did not impact nest predation in this environment. We suggest that future studies on artificial nests should incorporate variations in nest types and validate the selection of egg types.

KEY WORDS. Breeding success, dome-shaped nests, Neotropical birds, nest predation, restinga.

INTRODUCTION

Birds build nests to protect themselves, their offspring, and their eggs from adverse weather conditions and predation (Gill 1994, Martin 1998, Hansell 2000, Winkler 2016). However, most of them have shown low reproductive success (Green 2004, França et al. 2016). The primary cause of this failure is nest predation (Mezquida and Marone 2001, Chalfoun and Martin 2007, Maziarz et al. 2019, De Aguiar et al. 2022), which has important consequences for the structure and functioning of communities (Ricklefs 2003, Biancucci and Martin 2010, Roper et al. 2010).

Intrinsic factors related to nest type or egg characteristics can have a direct or indirect impact on nest success (Borges and Marini 2010, Dias et al. 2010, Matysioková and Remeš 2022). Predation rates tend to be higher in cup-shaped nests than in dome-shaped nests (Martin and Li 1992, Purcell and Verner 1999, França et al. 2016). The higher predation

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rate in open nests is due to easier visibility and access to nest contents by predators (Oniki 1979, Mainwaring et al. 2015), considering birds, mammals, and snakes as the primary nest predators (Duca and Marini 2004, Robinson et al. 2005, Conner et al. 2010). Certain predatory bird species, especially passerines, are efficient at nest detection in open habitats (França et al. 2009, Dodonov et al. 2017), while mammals exhibit greater proficiency to locate ground nests (Mezquida and Marone 2002, Pretelli et al. 2023). These patterns of nest predation dependent upon nest type or nest habitat have rarely been tested in tropical regions (Marini 2017).

Alongside nest shape, the size and color of avian eggs influence their vulnerability to predation. Research suggests that smaller eggs are more likely to be depredated due to their fragility and attractiveness to a wider range of predators (Brouwer and Spaans 1994, Degraaf et al. 1999, Maier and Degraaf 2000, Alvarez and Galetti 2007). Egg crypsis and camouflage often favor nest survival, particularly among ground-nesting shorebirds, by minimizing detection by predators (Skrade and Dinsmore 2013, Troscianko et al. 2016). In contrast, the impact of egg color variation on nest predation in small cup-shaped passerine nesters is unclear (Weidinger 2001, Kilner 2006). Understanding these predation patterns is crucial for designing artificial nest experiments (Major and Kendal 1996, Degraaf et al. 1999, Yang et al. 2016).

Studies estimating predation rates often use artificial nests for their advantages, such as variable control and ease of conducting experiments compared to natural nests (Marini et al. 1995). However, these experiments have faced criticism for differing predation rates compared to natural nests (Zanette 2002, Burke et al. 2004, Faaborg 2004, Mouton and Martin 2019), with the type of egg used being cited as a contributing factor (Wilson et al. 1998). These experiments typically use Japanese quail, *Coturnix japonica* Temminck & Schlegel, 1848, eggs. However, some studies have demonstrated differences in their characteristics (e.g., size, color, and texture) compared to the eggs of certain passerines, as well as the ineffectiveness of some predators to detect and prey upon them (Roper 1992, Haskell 1995a, Marini and Melo 1998).

To address misconceptions about quail eggs, researchers have turned to alternative egg types like atlantic canary, *Serinus canaria* (Linnaeus, 1758) (Alvarez and Galetti 2007), chestnut-bellied seed-finches, *Sporophila angolensis* (Linnaeus, 1766), and white-rumped munia, *Lonchura striata* (Linnaeus, 1766), eggs (Oliveira et al. 2013). Some have also used synthetic eggs made of materials like modeling clay, wax, or plasticine for better results (Zanette 2002, Alvarez and Galetti 2007, Pretelli et al. 2023). So far, synthetic eggs are the closest representation of natural eggs, but differences like odor and consistency can still affect predation likelihood (Haskell 1995b, Maier and Degraaf 2001). Therefore, there are gaps regarding the most appropriate model for artificial nest experiments since all have advantages and disadvantages.

Although potential issues exist, the use of Japanese quail eggs has been the most practical option so far due to their easy availability and size similarity to small and medium-sized birds (Cembrano et al. 2021). However, other quail species, like blue-breasted quails, *Synoicus chinensis* (Linnaeus, 1766), offer different egg types suitable for field experiments (Batáry et al. 2014). This species lays eggs with various solid colors (white, brown, green) and lengths 22–25 mm, contrasting with Japanese quail eggs, which have a mottled camouflage coloration and lengths 25–30 mm (authors' measurements, n = 30 eggs of each type). Consequently, Blue-breasted quail eggs may better represent the size, color, and shell texture of wild passerine eggs, providing a potential solution to issues associated with egg types.

In this study, we examined the impact of nest and egg types on the survival of artificial nests in a costal shrubland in southeastern Brazil. Specific objectives included: i) assessing and comparing survival rates between two nest types, cup-shaped and dome-shaped; ii) evaluating and comparing survival rates between the egg types of Japanese quail and blue-breasted quail eggs. We tested the hypotheses that: (1) nest type affects artificial nest survival, with the expectation that dome-shaped nests are more successful than cup-shaped nests (França et al. 2016, Mouton and Martin 2019); (2) egg type affects artificial nest survival, with the prediction that the cryptic and bigger Japanese quail eggs are more successful than Blue-breasted quail eggs (Degraaf et al. 1999, Yang et al. 2016).

MATERIAL AND METHODS

Study area

The data was collected in the Parque Estadual Paulo César Vinha (PEPCV), located in the municipality of Guarapari, Espírito Santo, southeastern Brazil (Fig. 1). PEPCV covers approximately 1,500 ha of land with a perimeter of 25 km, extending from the ES-060 state highway to the east to the Atlantic Ocean (20°35'08.91"S, 40°25'01.86"W). It shares its northern and southern boundaries with the urban areas of the municipalities of Vila Velha and Guarapari, respectively. The climate in the region, classified according to the Köppen-Geiger system, is tropical monsoon (Am), with

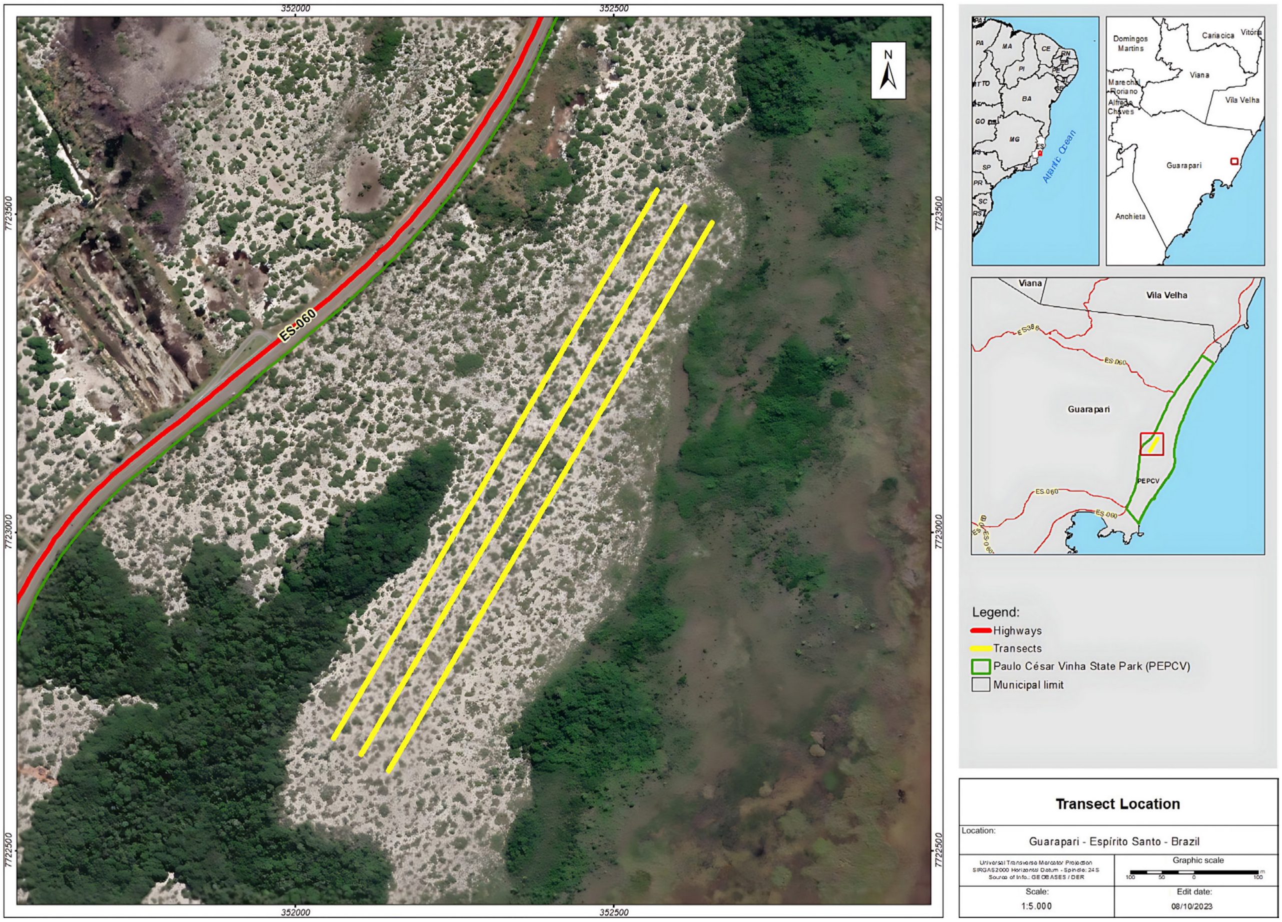

Figure 1. Location of the study area within the municipality of Guarapari, in the state of Espírito Santo, southeastern Brazil (upper right). The green polygon (right) represents the boundaries of Paulo César Vinha State Park, while the red line (left) indicates the ES-060 state highway. The yellow lines (left) mark the locations of the three transects within the Non-Floodable Open Shrubland vegetation, where data collection occurred.

an average annual temperature of 23.3 °C and an average annual precipitation of 1,307 mm (Alvares et al. 2013).

PEPCV boasts the largest area of coastal shrubland (restinga) vegetation along the southern coast of Espírito Santo, featuring a mosaic of forest formations typical of these environments. It is one of the few conservation units situated within the coastal zone of the state (Venturini et al. 1996). The Non-Floodable Open Shrubland vegetation, which covers most of the PEPCV area and is easily accessible, was chosen for this study.

Data collection

The cup-shaped artificial nests were crafted from spirally arranged and aligned grass bundles to prevent disintegration. Dome-shaped artificial nests were formed by combining two cup-shaped nests, securely sewn together with an opening on one side (Fig. 2A). The nests were bathed in muddy water to reduce human scent clues. After that, the nests and eggs were handled with latex gloves.

We conducted two simultaneous experiments from August 16–31, 2017. The first experiment assessed the impact of nest type (cup-shaped and dome-shaped nests) using 100 nests containing one Japanese quail egg each, evenly divided into 50 cup-shaped and 50 dome-shaped nests. In the second experiment, we assessed the effect of two distinct egg types (Fig. 2B). We used the same 50 cup-shaped nests with Japanese eggs from the first experiment, and another set of 50 cup-shaped nests with blue-breasted quail eggs.

We arranged the nests across three 1-km transects spaced 50 m apart (Fig. 1). Within each transect, 50 nests

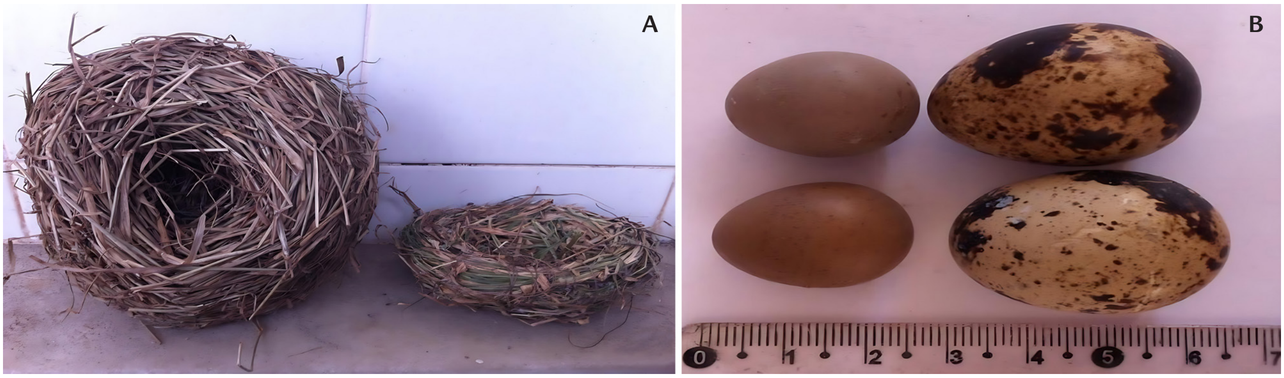

Figure 2. Photographs with types of nests and eggs used in the experiment: (A) two types of nests (dome and cup-shaped) used in the experiment; (B) Depicting the eggs of both quail species: on the left, smaller eggs of *Synoicus chinensis* in shades of brown and dark gray, while on the right, the speckled and camouflaged eggs of *Coturnix japonica*.

were alternated, with one cup-shaped nest containing a blue-breasted quail egg, followed by one dome-shaped nest, and then another cup-shaped nest, each equipped with a Japanese quail egg. We positioned the nests equidistantly at 20 m intervals (e.g., Duca et al. 2019, Silva et al. 2019, De Aguiar et al. 2022). The nests were attached to shrubs 1.5 m above the ground.

The nests were exposed to the risk of predation for a period of 15 days, which corresponds to the average incubation period of birds in the study site (e.g., Daros et al. 2018, Morais et al. 2019, Dutra et al. 2021). We conducted regular visits, spaced three days apart, to monitor the nests and assess their contents (whether preyed upon or intact). A nest was classified as depredated when its eggs were damaged or removed.

Data analyses

The daily survival rate (DSR) is defined as the probability of a nest surviving for one day within a specific time interval (Dinsmore et al. 2002). We used the 'nest survival' function in the MARK program (Cooch and White 2024) to model the DSR of artificial nests based on nest and egg types. Survival modeling in the MARK program requires four parameters to be met: 1) the day the nest was encountered; 2) the last check day when the nest was not predated; 3) the last check day for the nest; 4) the fate of the nest: predated or intact. Since we used artificial nests, the encounter day was always the first experimental day. Each nest's record lasted from day 1 (the first experimental day) to day 16 (the last experimental day), which corresponds to the eggs' exposure time to predation.

We treated each set of 50 nests within the transects as a separate group in our models: i) group 1, cup-shaped nests with Japanese quail eggs; ii) group 2, dome-shaped nests with Japanese quail eggs; iii) group 3, cup-shaped nests with blue-breasted quail eggs. The models considered were the null model (.) and the group model (g). The null model assumes constant survival across groups, while the group model represents the effect of nest type and egg type.

We formulated models by grouping the various groups in different combinations to assess the impacts of nest type and egg type. These models were organized into three steps. In the initial step, we evaluated the models (g1–2, 3) and (g1–3, 2). The model (g1–2, 3) examined the effect of egg type on survival rates by treating groups 1 and 2 as a combined unit (g1–2, nests with Japanese quail eggs) and group 3 as a separate unit (g3, nests with blue-breasted quail eggs). The model (g1–3, 2) examined the effect of nest type on survival rates by treating groups 1 and 3 as a combined unit (g1-3, cup-shaped nests) and group 2 as a separate unit (g2, dome-shaped nests). In the next step, we treated group 1 as one unit and group 2 as another (g1, g2), examining the effect of nest type. Finally, in the third step, we regarded group 1 as one unit and group 3 as another (g1, g3) to investigate the influence of egg type on cup-shaped nests only (Table 1). We ranked the models based on the values of the Akaike Information Criterion (AIC), where models with $\Delta AIC \leq 2$ were considered to have similar capacity to explain the variation in the dataset (Burnham and Anderson 2002).

In order to compare our results with those obtained without utilizing the 'nest survival' function in the MARK program, we compared the apparent success of the nests (percentage of successful nests) (Skutch 1966) across nest types and egg types using two-way Chi-Square (χ^2) tests using a 2 x 2 Contingency Table (Silveira Neto et al. 1976) in the BioEstat 5.3 program (Ayres et al. 2000) ($\alpha = 0.05$).

RESULTS

Most nests (66%) were predated across experiments (n = 150). Apparent success was higher in dome-shaped nests (52%, n = 50) compared to cup-shaped nests (22%, n = 50) (χ^2 = 9.65; df = 1; p = 0.002). However, apparent nest success did not differ between Japanese quail eggs (22%) and blue-breasted quail eggs (28%) in cup-shaped nests (χ^2 = 0.48; df = 1; p = 0.488).

These results were confirmed by nest survival models. Models that assessed the impact of nest type using data from both types of eggs [S (g1–3, g2)] (step 1) or exclusively Japanese quail eggs (step 2) explained 72% and 96% of the variation in nest daily survival rate (DSR), respectively (Table 1). Again, dome-shaped nests with Japanese or blue-breasted quail eggs were more likely to survive (DSR = 0.96) than cup-shaped nests (DSR = 0.92) (Table 2). In contrast, the constant model [S (.)] and the model including the effect of egg type considering data from both nest types [S (g1 –2, g3)] had little influence on the daily survival rate (DSR) of nests (ΔAIC > 2) (Table 1: step 1). The model that tested egg type exclusively in cup-shaped nests (step 3) explained just 27% of the variation in nest DSR and performed less effectively than the constant model (Table 1: step 3).

Table 1. Model selection for artificial nest survival (S) based on the Akaike Information Criterion (AICc). For each model, we calculated Akaike weight (wi), the number of parameters (K), and the deviance. The numbers represent distinct groups indicating the effects of nest and egg types, where (g1) corresponds to cup-shaped nests with Japanese quail eggs, (g2) to dome-shaped nests with Japanese quail eggs, and (g3) to cup-shaped nests with Blue-breasted quail eggs. In step 1, all three groups were considered, while in steps 2 and 3 we isolated the effects of nest type and egg type, respectively.

Models	AICc	ΔAICc	wi	K	Deviance
Step 1					
S(g1-3, g2)	515.72	0.00	0.72	2	511.71
S(g)	517.73	2.00	0.26	3	511.71
S(g1-2, g3)	524.00	8.28	0.01	2	519.99
S(.)	524.85	9.13	0.01	1	522.85
Step 2					
S(g1, g2)	346.10	0.00	0.96	2	339.09
S(.)	349.37	6.27	0.04	1	347.37
Step 3					
S(.)	362.79	0.00	0.73	1	360.78
S(g1, g3)	364.79	2.01	0.27	2	360.78

Table 2. Daily Survival Rate (DSR) estimated by the group effect model [S (g)], wherein: SE stands for standard error, CI represents confidence interval, and 'Nest success' denotes nest success within the groups (1, 2, and 3). Group 1 pertains to cup-shaped nests with Japanese quail eggs, Group 2 to dome-shaped nests with Japanese quail eggs, and Group 3 to cup-shaped nests with Blue-breasted quail eggs.

Groups	DSR	SE	CI	Nest success (%)
1	0.922	0.012	0.895 - 0.942	29.6
2	0.962	0.008	0.943 - 0.974	55.9
3	0.921	0.013	0.942	29.1

DISCUSSION

The predation rate found in our study (66%) was similar to that found for natural nests in the same coastal shrublands (Daros et al. 2018– 66.7%, Araujo 2016 –62.2%, Dutra et al. 2021 – 68.1%). This result shows the viability of artificial nest experiments to assess the predation risk. Particularly, these experiments have become a good tool to test hypotheses where the control of variables is fundamental to shed light on the response variables.

Our results support the hypothesis of higher survival of dome-shaped nests compared to cup-shaped nests. This finding is consistent with results from other studies on both natural and artificial avian nests in the Neotropical region (Robinson et al. 2000, Arantes and Melo 2011, França et al. 2016, Mouton and Martin 2019). The higher survival of dome-shaped nests is likely attributed to poor visibility and predators' reduced access to nest contents (Oniki 1979). Birds have been considered the primary nest predators in open areas with shrub vegetation (Söderström et al. 1998, França et al. 2009, Dodonov et al. 2017), and there is strong evidence of birds as the main nest predators in our study site (Daros et al. 2018). Therefore, closed nests may reduce predation efficiency by visually oriented individuals such as birds, as the eggs are not exposed.

Nest survival was not influenced by egg type, thus not supporting the hypothesis that larger Japanese quail eggs are more likely to survive than smaller blue-breasted quail eggs. This result differs from those commonly reported in the literature, where smaller eggs are often more vulnerable to predation due to their fragility and susceptibility to a wider range of predators (Degraaf et al. 1999, Maier and Degraaf 2000, Alvarez and Galetti 2007). One possible explanation for our result is the high density and diversity of predators in the study area (Reitsma et al. 1990), with predators of different sizes preying upon nests with varying egg sizes due to morphological constraints, for example (Oliveira et al. 2013, Maier and DeGraaf 2001).

A second explanation could be that the similar conspicuousness of both types of eggs in cup-shaped artificial nests may result in similar detectability by visually-oriented predators (Söderström et al. 1998, França et al. 2009). Alternatively, egg size may have still influenced nest survival, but this effect might have been counterbalanced by the effect of egg color on predation rates. The cryptic coloring of Japanese quail eggs may offset the negative effects of their larger size on nest survival (Lovell et al. 2013, Skrade and Dinsmore et al. 2013, Troscianko et al. 2016). In contrast, blue-breasted quail eggs, with their diverse and uniform colors, may be more conspicuous to predators and counterbalance the increase in survival conferred by their smaller size (Yang et al. 2016).

Our results emphasize the importance of taking nest type into account in artificial nest experiments. Many such studies primarily focus on cup-shaped nests (Major and Kendal 1996, Söderström 1999), especially in the Neotropics (Oliveira et al. 2013), overlooking potential ecological factors that could affect the survival of dome-shaped or closed nests. While our findings do not definitively clarify whether egg size and/or color influence artificial nest survival, they suggest that these factors may not play a significant role in determining nest survival in our study area. Therefore, simply controlling egg size may not be enough to make predation experiments with artificial nests more realistic in coastal shrublands. We suggest future studies focus on identifying and comparing nest predator communities in open tropical habitats (Thompson III and Burhans 2004) to better understand why egg characteristics may not relate to predation probability in these environments. Future research could involve independent manipulations of egg coloration and size to better understand their impact on nest survival (Yang et al. 2016).

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