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Highway effects on artificial nest survival in a neotropical sand-coastal plain: A spatiotemporal approach

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ABSTRACT

Roads are a leading cause of habitat fragmentation and may reduce bird populations by increasing nest predation rates. However, few studies have investigated the effects of traffic volume on the reproductive success of roadside birds in the neotropics. Our goal was to evaluate the effects of spatial, temporal, and vehicle flow variations on the survival of artificial open-cup nests. The study was carried out in a nature reserve on the side of a highway during the breeding season (from October to March) in two restinga (sand-coastal plain) phytophysiognomies in southeastern Brazil: non-floodable (open) and floodable (closed). One hundred thirty nests were distributed along transects ranging from 3 m to 300 m from the highway in each vegetation type (totaling 260 nests). The nests were checked every three days for their status (depredated or intact) over 12 days, and new nests were subsequently placed near sampling points of depredated or successful nests. We estimated survival using logistic exposure generalized linear and additive mixed models. At the end of the 180 days of the experiment, 33% of 6202 nests were successful. Nest survival was higher in open restinga than in closed restinga. In both habitats, nest survival was lowest mid-season and highest at the beginning and end. Survival rates peaked near the highway, declined up to 50 m away, then showed a slight increase. Finally, survival increased at moderate-to-high traffic volumes (~22,000 vehicles/day), particularly in open restinga. We suggest that spatial, temporal, and habitat-specific highway impacts (e.g., noise, vibration, visual stimuli) can lead to variations in the activity of nest predators, generating fluctuations in nest survival associated with predator behavior.

1. Introduction

Nest predation is a crucial factor in reducing avian population sizes (Jokimäki and Huhta, 2000; Henschke et al., 2016), contributing to an average of 80% nesting failures (Martin, 1993; Latif et al., 2012). Some factors, such as temporal and spatial variations throughout the breeding season, directly or indirectly influence nest predation, impacting the reproductive success of birds. Temporal factors are linked to nest age and timing in the breeding season (Thompson-III, 2007; Wilson et al., 2007; França and Marini, 2009a; Zhao et al., 2020), while spatial factors involve habitat characteristics, nest density, or nest location (Burhans et al., 2002; Roos, 2002; Peak et al., 2004; Shitikov et al., 2018).

Nest predation is known to increase during the breeding season due to heightened predator activity in search of more abundant prey (Verhulst and Nilsson, 2008; Duca et al., 2019). These predators may develop a "search image" after previous predatory experiences, involving selectively seeking a more abundant prey type encountered repeatedly (Dukas, 2002; Ishii and Shimada, 2010). In contrast, nest predation may decrease in the middle of the breeding season in response to the "dilution effect". This mechanism involves a reduction in predation risk due to increased prey availability (Delm, 1990; Duca et al., 2019; Gorosito et al., 2024).

Habitat selection may be determinant to nest survival when predation risk and/or availability of food resources have high predictability (Pleszczynska, 1978). Certain bird species choose breeding territories with lower predator activity (Arlt and Part, 2008), though predators

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may relocate to areas with higher prey density (Soderstrom et al., 1998). For example, nest predation rates are often high at habitat edges, as predators residing nearby select these locations for foraging (Ries and Sisk, 2004; Arbeiter and Franke, 2018). However, contrasting results have been found in other studies, such as the absence of an increase in predation rates at the edges of forest fragments compared to the interior (Watson et al., 2004; França and Marini, 2009b; Luo et al., 2017).

While many studies have assessed the edge effect on bird reproduction (Batáry and Báldi, 2004; Luo et al., 2017; Valentine et al., 2019), the majority have focused on forest edges associated with pastures or other vegetative structures. There is limited information on areas fragmented by roads and highways (Forman et al., 2003; Coffin, 2007; Pescador and Peris, 2007; Fahrig and Rytwinski, 2009; Silva et al., 2019). Road construction is a major cause of forest fragmentation (Coffin, 2007; Laurance et al., 2009), leading to pronounced edge effects, including vehicle traffic, mortality, and noise (Goosem, 2007; Summers et al., 2011; Khamcha et al., 2018), often causing deleterious impacts on local species (Van der Ree et al., 2015; Silva et al., 2023).

Vehicle traffic, for example, can both increase or decrease nest survival near edges by influencing predator habitat use (Pescador and Peris, 2007; Yamac and Kirazli, 2012; Rytwinski and Fahrig, 2013; Rao and Koli, 2017). The effect of road edges on avian nest predation varies widely (Vetter et al., 2013), with some predator species unaffected or even benefiting from roads (DeGregorio et al., 2014; Downing et al., 2015; Khamcha et al., 2018). This effect is less evident on roads with medium or low traffic intensity (Pescador and Peris, 2007) or unpaved roads (Yamac and Kirazli, 2012; DeGregorio et al., 2014). While some studies have explored highway-affected environment edges (Pescador and Peris, 2007; DeGregorio et al., 2014; Silva et al., 2019), there is still a lack of information on the factors that influence nest predation and the reproductive success of birds in these locations, especially in tropical contexts (Rosa and Bager, 2012; Vetter et al., 2013; Angkaew et al., 2019), with many gaps and questions to be answered. Understanding these factors is useful for conservation decision-making and territorial planning, particularly in managing conservation units facing challenges from such developments (Trombulak and Frissel, 2000; Rosa and Bager, 2012; Vetter et al., 2013; Khamcha et al., 2018).

Artificial nests are widely used to estimate predation rates due to their methodological advantages, including variable control and experimental ease (Marini et al., 1995). They enable the standardization of key traits (e.g., size, placement, materials) (King et al., 1999; Moore and Robinson, 2004) and facilitate assessments of environmental factors affecting nest survival, such as habitat edges, vegetation structure, and proximity to roads (Burhans et al., 2002; Roos, 2002; Pescador and Peris, 2007; De Aguiar et al., 2022). Additionally, they minimize disturbance to wild bird populations (Major and Kendal, 1996; Weidinger, 2002). Studies from the Brazilian sand-coastal plain reporting similar predation rates between artificial and natural nests further support their reliability for assessing predation risk (Daros et al., 2018; Dutra et al., 2021; Silva et al., 2024).

We assessed the impact of a highway on artificial nest survival along a gradient from the road to 300 m into the interior of two sand-coastal plain (restinga) phytophysiognomies (Open Shrubby Formation not floodable and Floodable forest) within a nature reserve in southeastern Brazil. Analyzing the nest survival variation across a distance gradient from the highway, we aimed to determine the effect (positive, neutral, or negative) and the extent to which these effects were observed (i.e., the distance from the highway) within both vegetation types. Additionally, we examined direct factors related to daily vehicle traffic variations on artificial nest survival, considering increased traffic during the summer tourism season that coincides with the middle of the breeding season of most bird species at the study site. Finally, we explored whether nest survival varied with the breeding season date.

We predicted a higher or lower artificial nest survival near the highway edges than in the interior of the restinga, considering that predators may be repelled or attracted by the highway (Khamcha et al., 2018; Silva et al., 2019). We also predicted a lower survival rate in Open Shrubby Formation not floodable compared to the Floodable forest, as habitat openness often makes the nests more visible and then vulnerable to visual predators (Coates and Delehanty, 2008; De Aguiar et al., 2022). Our third prediction was that vehicle traffic flow would influence nest survival through the positive or negative effect on the use of highway-side edges by predators (Pescador and Peris, 2007). Finally, we expected a decrease in nest survival as the breeding season progresses, as suggested by the "predator search image" hypothesis (Dukas, 2002; Verhulst and Nilsson, 2008; Duca et al., 2019), or an increase in mid-season followed by a decline toward the end of the season, as predicted by the dilution effect (Turner and Pitcher, 1986; Delm, 1990; Duca et al., 2019).

2. Materials and methods

2.1. Study area and period

The data were collected in Paulo César Vinha State Park (PEPCV), located in Guarapari, state of Espírito Santo, southeastern Brazil (Fig. 1; Appendix Fig. S1). Spanning 1500 ha along a 25-km perimeter from the ES-060 state highway to the Atlantic Ocean (20°33'–20°38' S, 40°23'–40°26' W), PEPCV shares borders with urban areas of the municipalities of Vila Velha and Guarapari. The climate is monsoon tropical (Am) (Köppen-Geiger system), with an average temperature of 23.3 °C and annual precipitation of 1307 mm (Alvares et al., 2013). PEPCV has the largest coastal plain vegetation area in southern Espírito Santo, with a mosaic of forest and shrubby formations, making it a rare nature reserves in the coastal zone (Pereira, 1990; Venturini et al., 1996).

The Open Shrubby Formation not floodable (hereafter 'open restinga') and the Floodable forest (hereafter 'closed restinga') were selected for this study based on their distinct vegetation characteristics, proximity to the highway, and accessibility. Open restinga, the predominant vegetation type in the study area, consists of sparse clusters of dense shrubs interspersed with nearly bare soil. These clusters vary in shape (rounded to elliptical) with irregular edges, reaching heights of up to 6 m and an average density of 9.8 clusters per 20 × 30-m sub-plot (Kuster et al., 2019). Typically, a central arboreal element, often from the *Clusia* genus, is surrounded by densely packed shrubs and herbaceous plants, transitioning into sparse grasses at the edges. Vegetation cover is approximately 53% (Kuster et al., 2019). The open restinga can be further divided into sandy areas with sparse herbaceous vegetation and vegetation islands, corresponding to the innermost sandy ridges (Pereira et al., 2004). The closed restinga has a closed canopy, averaging 20 m in height, with some emergent trees. The understory includes lianas, shrubs, and herbs, with dense leaf litter. Nevertheless, emergent trees are relatively scarce (Cepemar, 2007).

The artificial nest experiment (see below) took place along the ES-060 highway from October 2017 to March 2018, covering 180 days, including the breeding season of most birds in the study area (Daros et al., 2018; Morais et al., 2019; Dutra et al., 2021), and months of varying vehicle traffic (Rodosol, 2017). This is a dual-lane paved road with a width of 16 m. It includes a central median of 4 m and a side median of approximately 3 m, covering the entire length bordering the PEPCV. Daily vehicle traffic averages 10,000 during the low tourist season, rising to 19,000 vehicles per day in the high tourism season (summer), especially in January (RodoSol, 2017). The speed limit along the entire stretch that crosses the reserve varies from 80 to 110 km/h depending on the type of vehicle.

2.2. Artificial nest experiment

We designed open cup-shaped artificial nests (100 mm diameter, 40 mm height) using spiral arrangements of grass bundles compressed against a shell mold, and stitched to prevent disintegration, representing typical open cup-nesting species (Silva et al., 2024). In the study area,

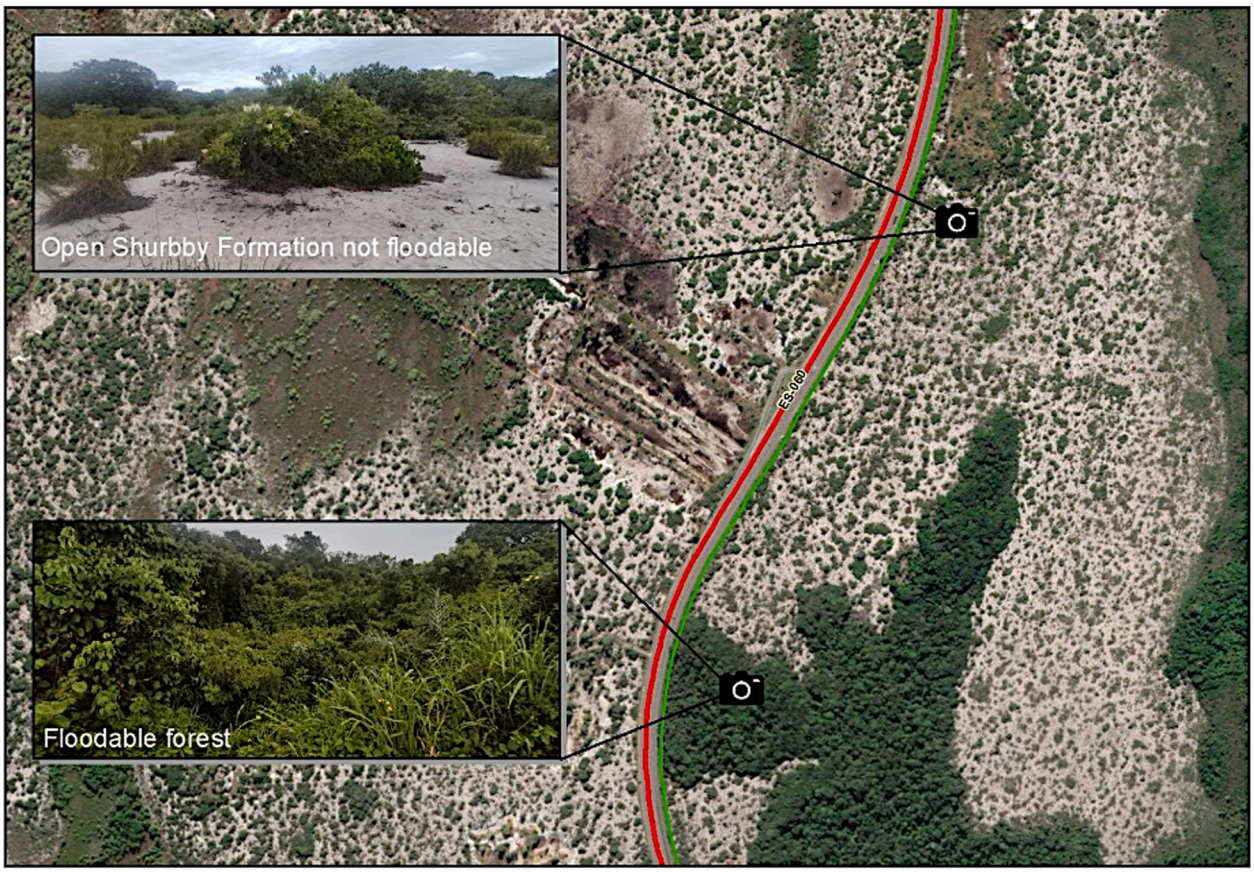

Fig. 1. Aerial photograph of the two physiognomies: Open Shrubby Formation not floodable (open restinga) and Floodable forest (closed restinga) where the experiments were implemented.

several bird species nest in open cup-shaped nests, including the Tropical Kingbird (*Tyrannus melancholicus*), Rusty-backed Antwren (*Formicivora rufa*), and the regionally threatened Tropical Mockingbird (*Mimus gilvus*), a key species of the restinga ecosystem (Daros et al., 2018; Morais et al., 2019; Dutra et al., 2021).

Twenty 300-m transects were established, 10 in open restinga and 10 in closed restinga (Fig. 1, Appendix Fig. S1). The areas were separated by 500 m, with transects in each area spaced 25 m apart. Each transect was marked with 13 sampling points at distances of 3, 25, 50, 75, 100, 125, 150, 175, 200, 225, 250, 275, and 300 m from the highway, extending towards the interior of the areas. This experimental design likely captures substantial variation in highway-driven disturbances on wildlife along the transect (e.g., wildlife-vehicle collisions, noise, and artificial light at night) (Summers et al., 2011; Khamcha et al., 2018). At each sampling point, an artificial nest with a Japanese Quail (*Coturnix japonica*) egg was initially placed, totaling 130 nests in each vegetation type and 260 nests across the study area. Each nest was numbered within its respective transect for identification.

The nests were positioned in shrubs at an approximate height of 1.5 m above the ground and marked with colored plastic tape placed 5 m away, facilitating their location during monitoring. The status of the nests (depredated or intact) was checked through regular visits every three days. Each nest was monitored for a 12-day cycle, corresponding to the average incubation period of common open-cup nesting passerines in the study area (Daros et al., 2018; Morais et al., 2019; Dutra et al., 2021). If no evidence of predation was observed after this period, the nest was moved to another location near the original sampling point in the same transect. A new egg was placed in the nest at the new location, considering it as a new one. In cases of predation during the 12-day cycle, the nest was also relocated, a new egg was added, and the new nest was exposed until predation occurred again or the 12-day period was completed. This procedure was repeated throughout the 180-day experiment, optimizing nest usage and increasing the sample size.

2.3. Traffic flow

To assess nest survival variations from highway effects, we used daily vehicle traffic data toll booth provided by Rodosol, the company responsible for the highway concession at that time (RodoSol, 2017). This toll booth was located on the ES-060 state highway, approximately 5 km from the study area. For each nest, we computed traffic flow as the average number of vehicles passing through the highway toll booth in Guarapari from the day that specific nest was placed until the last day that nest was observed active (i.e., with any intact egg).

2.4. Data analyses

All analyses were conducted using R (R Core Team, 2023). We employed Generalized Linear Mixed Models (GLMM, binomial error family) from the 'lme4' R package (Bates et al., 2014) or Generalized Additive Mixed Models (GAMM, binomial error family) from the 'mgcv' package ('bam' function) (Wood, 2011), both with logistic exposure (Shaffer, 2004) to assess the effects of covariates on daily nest survival (Cockle et al., 2015). The logistic exposure model is a logistic regression with a modified logit link that controls for the effect of the number of days the nests were exposed to predation (i.e., exposure time). We used the model link function developed by Bolker (2019) to account for the effect of nest exposure days on survival probability. For successful nests, exposure time was the number of days from deployment to the last day the nest was active, while for depredated nests, we added the average number of days between the last observed active day and the first day the nest was checked after predation (Ludwig et al., 2012; Seibold et al.,

2013).

The analyses were conducted in two stages to prevent overfitting and facilitate result interpretation. In Stage 1, we used GLMM to compare nest survival between habitat types, with nest fate as the response variable (0 = depredated, 1 = success). Habitat type was included as the single explanatory variable, and transect identity was added as a random intercept. In Stage 2, we used GAMM to assess the additive effects of three covariates (nest deployment date, mean traffic flow, and distance from the highway) on nest survival in each habitat type separately. Nest deployment date was defined as the ordinal day since the first deployment (day 1: 03 October 2017). The response variable remained nest fate (0 = depredated, 1 = success), and transect identity was included as a random intercept.

To assess whether nest fate was better modeled with a parametric (linear) or smooth (nonlinear) function for each covariate, we built multiple versions of the GAMM. In each model, we replaced the linear term of one covariate at a time with a smooth term while keeping the other two covariates as linear terms. We then compared these model pairs (parametric vs. smooth for each covariate) using likelihood ratio tests and the Akaike Information Criterion (AIC), selecting the model with the lowest AIC as the best-fitting model (Symonds and Moussalli, 2011). This process was repeated for each covariate. The final model for each habitat type was the one that provided the best fit (parametric or smooth) for each covariate.

3. Results

At the end of the 180-day experiment, 33% out of 6202 nests were successful. Success rates were 35% for the 2955 nests in open restinga and 31% for the 3247 nests in closed restinga. The logistic exposure GLMM revealed lower nest survival probability in closed restinga compared to open restinga (β [95% CI] = −0.19 [−0.268, −0.112], $p <$ 0.0001). The estimated daily survival rate was 0.81 for nests in closed restinga and 0.84 in open restinga.

Nest survival probability exhibited a non-linear relationship with all three covariates in both habitat types (Tables 1 and 2). In both habitats, survival declined sharply toward mid-season before increasing again toward the end of the study, returning to initial levels (Fig. 2A–D; Appendix Fig. S2A). This seasonal effect was more pronounced and shorter in duration in the open restinga (Fig. 2A) than in the closed restinga (Fig. 2D; Appendix Fig. S2A).

Nest survival was highest near the highway, declined up to 50 m away, then fluctuating and slightly increasing between 75 and 300 m in both habitats (Fig. 2B–E; Appendix Fig. S2B). Survival also increased with traffic volume, with stronger effects in open restinga (Fig. 2C–F; Appendix Fig. S2C). Nest survival peaks occurred at low-to-moderate (~13,000 vehicles/day) and especially moderate-to-high (~22,000 vehicles/day) traffic levels, while very high traffic (~23,000–25,000 vehicles/day) was associated with lower survival, particularly in closed restinga. Survival was also reduced at low (~9000 vehicles/day) and low-to-moderate (~13,000 vehicles/day) traffic levels (Fig. 2C–F; Appendix Fig. S2C).

Table 2
Smooth terms for the logistic exposure GAMM predicting artificial nest survival in open restinga and closed restinga in relation to date in the breeding season, distance from the highway, and vehicle traffic flow.

Habitat type	Smooth terms	Edf	Ref.df	χ^2	p
Open restinga	Date	8.85	8.99	570.83	<0.0001
	Distance	7.30	8.31	89.34	<0.0001
	Vehicle traffic	8.82	8.99	807.77	<0.0001
Closed restinga	Date	8.77	8.98	691.80	<0.0001
	Distance	8.77	8.98	249.90	<0.0001
	Vehicle traffic	8.85	8.99	943.1	<0.0001

Transect identity was added as a random intercept in all models. Edf: effective degrees of freedom. Ref.df: reference degrees of freedom.

4. Discussion

This study analyzed the spatial and temporal patterns of artificial nest survival on a Neotropical sand-coastal plain, assessing the effects of a high-traffic highway. We performed experiments with 6202 artificial nests over 180 days of monitoring, demonstrating that nest survival was higher in the open (35%) than in closed (31%) vegetation, contrary to findings based on nest visibility (Coates and Delehanty, 2008; de Aguiar et al., 2022). Survival was lowest in the middle of the breeding season, with the highest values at the beginning and end of the study period, suggesting the influence of the "predator search image" in the first half of the experiment period (Verhulst and Nilsson, 2008; Duca et al., 2019). The survival was also higher near the highway, corroborating past findings (Khamcha et al., 2018; Silva et al., 2019). Another finding was that survival increased under moderate to high traffic volumes (Pescador and Peris, 2007), especially in the open restinga. This result suggests that traffic-associated factors, such as noise and visual disturbances, may influence predator activity and, consequently, nest predation rates.

4.1. Vegetation type, vehicle traffic flow, and nest survival

We found a slightly lower survival of artificial nests in closed than open restinga habitats. However, several studies in areas not adjacent to highways found lower nest survival in open than in closed habitats (e.g., Martin, 1993; Stokes and Boersma, 1998; de Aguiar et al., 2022). Our result, therefore, contradicts the hypothesis that nest visibility increases nest predation in open habitats (Coates and Delehanty, 2008; de Aguiar et al., 2022). An explanation for our results may lie in the increased abundance and/or richness of predators within the closed restinga habitat (Reitsma et al., 1990; Soderstrom et al., 1998; Dion et al., 2000; de Bortolo et al., 2021). For instance, denser or floodable forests may enhance predation rates by providing more microhabitats for small mammals and monkeys, even if it reduces nest visibility (Batáry et al., 2014). In closed restinga, potential nest predators include marmosets (*Callithrix* sp.) (Ballarini et al., 2021), the Big-eared Opossum (*Didelphis aurita*), and the Bare-tailed Woolly Opossum (*Caluromys philander*) (de Bortolo et al., 2021). The marmosets are diurnal predators, but the other two have nocturnal habits guided mainly by smell. One issue that could be further investigated is whether predation in the closed restinga is

Table 1
Results of likelihood ratio tests (LRT) and AIC values comparing logistic exposure GAMMs for artificial nest survival in open and closed restinga.

Habitat type	Covariate	AIC (linear)	AIC (nonlinear)	Deviance	df	p
Open restinga	Date	5981	5109	887.75	8.09	<0.0001
	Distance	5981	5854	140.99	7.97	<0.0001
	Vehicle traffic	5981	5224	772.45	7.95	<0.0001
Closed restinga	Date	7017	6286	746.14	7.97	<0.0001
	Distance	7017	6414	618.53	8.09	<0.0001
	Vehicle traffic	7016	6090	940.33	7.61	<0.0001

Each covariate (breeding season date, distance from the highway, and vehicle traffic) was modeled as a parametric (linear) vs. smooth (nonlinear) term while keeping the other two covariates linear. Transect identity was included as a random intercept. df = degrees of freedom.

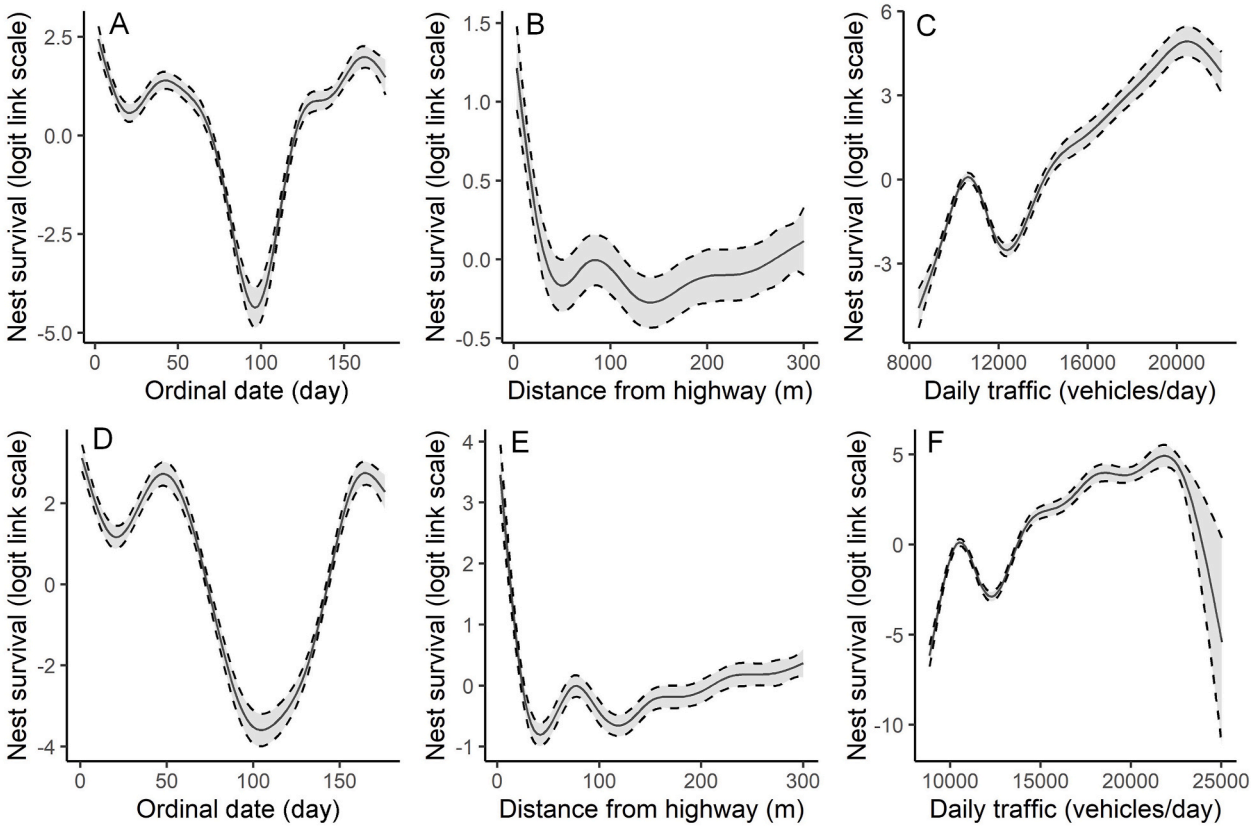

Fig. 2. GAMM predictions showing the partial effects of date (breeding season day; day 1 = 03 October 2017), distance from the highway (m), and daily traffic (average vehicle count during nest activity) on artificial nest survival. Models were built separately for Open Shrubby Formation not floodable (open restinga) (A, B, C) and Floodable forest (closed restinga) (D, E, F). Curves and shaded 95% confidence intervals were derived from the final models, including only smooth terms.

more associated with nocturnal than diurnal predators.

In contrast, the observed differences in nest survival between habitats are unlikely due to avian nest predators. Passeriformes, the primary nest predators in open Neotropical habitats (França et al., 2009; Menezes and Marini, 2017; Ribeiro-Silva et al., 2018), are more diverse and abundant in open restinga (Gomes et al., 2016), where key nest predators like the Guira Cuckoo (*Guira guira*) (Ballarini et al., 2021) and the Tropical Mockingbird (*M. gilvus*) also occur (Cody, 2020). Additionally, passerines may be unable to prey on larger Japanese Quail eggs (Maier and Degraaf, 2001; Oliveira et al., 2013). A simultaneous artificial nest experiment in our study area found no difference in predation between nests with Japanese Quail and Blue-breasted Quail (*Synoicus chinensis*) eggs, despite size differences (Silva et al., 2024), suggesting that non-passerine predators may drive variation in artificial nest survival.

Artificial nest survival increased with moderate-to-high traffic volumes, particularly in open habitat. Although we did not directly assess the effects of noise, traffic volume is a strong positive indicator of noise levels (Reijnen et al., 1997). Traffic volume and noise can influence the density of bird species and other animals that may prey on natural nests (DeGregorio et al., 2014; Silva et al., 2023). Traffic noise may mask predator cues for prey (Kern et al., 2016), but can also obscure prey cues for predators, reducing nest detection (Senzaki et al., 2016) and leading predators to avoid foraging near highways (Fröhlich and Ciach, 2017). Additionally, predators may avoid highways due to noise-induced physiological stress (Amjad et al., 2024) or the increased risk of vehicle collisions on high-traffic days (Husby, 2017).

The increased artificial nest survival at moderate-to-high traffic volumes may also partially explain the observed higher survival of artificial nests in open habitats. The open restinga amplifies the visual and acoustic impacts of highways on predator density and behavior (Reijnen et al., 1995, 1996; Parris and Schneider, 2009). Noise pollution, for instance, may spread more extensively in open habitats (Benítez-López et al., 2010; Van der Ree et al., 2015). Therefore, the presumed increased accessibility and visibility of nests to predators in open restinga (Coates and Delehanty, 2008; de Aguiar et al., 2022) may be counteracted by nest predators avoiding the larger noise-affected areas in this habitat.

4.2. Distance to highway and nest survival

The survival of artificial nests was higher at the immediate edge (<50 m) of the highway, regardless of the habitat type. Similar patterns of high nest survival at the immediate edge of the highway (25 m) were found, for example, in studies in the woodlands of the Iberian Peninsula (Pescador and Peris, 2007) and in a lowland Atlantic Forest (Silva et al., 2019). This result is less common in areas near highways with moderate and low traffic flow (Pescador and Peris, 2007) or on unpaved roads (Yamac and Kırazlı, 2012; DeGregorio et al., 2014).

Silva et al. (2019) discussed two hypotheses to explain the lower nest predation within 25 m of a heavily trafficked paved highway: the predation release hypothesis and the non-road-specific edge effects hypothesis. We suggest that these hypotheses may explain our results as well. The predation release hypothesis predicts negative effects of vehicle traffic on predators, leading to increased nest survival and abundance at the highway edges due to reduced predator abundance (Rytwinski and Fahrig, 2007, 2013; Fahrig and Rytwinski, 2009; Angkaew et al., 2019). As highlighted by Silva et al. (2019), road avoidance by birds and mammals—the main avian nest predators (França et al., 2009; Menezes and Marini, 2017)—is pervasive in open habitats (Fahrig and Rytwinski, 2009; Benítez-López et al., 2010) and may extend for hundreds of meters within forests (Forman and Deblinger, 2000;

Benítez-López et al., 2010). While we lack specific data to assess the impact of roadsides on the nesting abundance of birds, our findings indicated that nest predators tend to avoid the immediate vicinity of highways, providing partial support for the predation release hypothesis.

Alternatively, nest predators might avoid foraging near the highway due to non-road-specific edge factors (Silva et al., 2019). These factors may include alterations in microclimate and/or vegetation structure near habitat edges (Didham and Lawton, 1999; Harper et al., 2015), potentially influencing habitat selection and/or the choice of foraging sites by birds (McCollin, 1998). This hypothesis helps explain our results, especially considering that: (i) non-road-specific edge factors may be more relevant to forested habitats (Laurance et al., 2007; Dodonov et al., 2013; Khamcha et al., 2018); and (ii) nest survival was lower in closed restinga than in open restinga.

The stronger immediate edge effect (<50 m) in both habitats may result from road-specific factors that diminish more rapidly with distance, impacting mortality risk assessment or noise avoidance by predators (Forman and Deblinger, 2000; Benítez-López et al., 2010; Silva et al., 2019). However, beyond 50 m from the highway, the survival of artificial nests slightly increased with distance from the road in both habitats. This finding suggests that while nest predators appear to avoid roadsides, they could be favored by edge effects at distances between 100 m and 200 m, leading to increased nest predation. Several mechanisms could account for this pattern, including changes in microclimate and vegetation structure (i.e., habitat disturbance) up to 200 m from the highway (Magnago et al., 2015) reducing nest concealment for predators (Spanhove et al., 2014). Future studies are needed to untangle roadside and non-roadside effects on predator density and behavior, as well as nesting site selection by birds.

4.3. Temporal variation in nest survival

Nest survival was higher at the beginning and end of the study period, but declined mid-season in both environments, around 100 days after the study began. Our findings only partially align with other studies on both natural and artificial nests, indicating a decline in survival as the breeding season advances (Naef-Daenzer et al., 2001; Gotmark, 2002; Duca and Marini, 2005; Oberg et al., 2014; França et al., 2016). The reduced nest survival in the middle of the breeding season may be explained by the predator's search image hypothesis. This hypothesis predicts that as the season progresses, predators become more efficient in acquiring abundant resources, leading to increased nest predation rates (Pinheiro et al., 2002; Batalha and Martins, 2004; Verhulst and Nilsson, 2008; Duca et al., 2019). The increased availability of natural nests in the mid-breeding season in our study site (Daros et al., 2018; Morais et al., 2019) may contribute to developing a predator search image since this effect is density-dependent (Duca et al., 2019). A decline in real nest availability towards the end of the season could lead to reduced predator abundance, potentially explaining a lower nest predation rate compared to the mid-breeding season (Gunnarsson and Elmberg, 2008).

5. Implications

Our findings offer valuable insights into understanding spatial and temporal patterns related to nest survival across different vegetation types in the restinga. Additionally, they underscore the ES-060 highway as a significant threat to avian reproductive success, with impacts slightly varying depending on habitat type. Mitigation measures should include elevated roads or tunnels to reduce habitat fragmentation, strict speed limits (e.g., 60 km/h), and multifunctional noise barriers with fauna bridges to limit road access and facilitate wildlife crossings (Glista et al., 2009). Continued long-term studies are crucial to further elucidate the observed patterns and disentangle potential associations between highway effects, both temporal and spatial, on nest success and predation in protected areas influenced by highways. This effort contributes to a better understanding of biodiversity conservation issues and the mitigation of highway impacts on birds and their habitats.

CRediT authorship contribution statement

Gleidson Ramos da Silva: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Pedro Diniz:** Writing – original draft, Validation, Formal analysis, Data curation. **Charles Duca:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Ethics statement

This research was conducted according to ethics committee of Universidade Vila Velha (License number 74/2009).

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve readability and language of the work. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.avrs.2025.100264.

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