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Avian Behavior, Ecology, and Evolution

Nest site selection and nest survival in the Warbling Doradito are positively associated with nest concealment

La selección del sitio de nidificación y la supervivencia de los nidos de *Pseudocolopteryx flaviventris* se asocian positivamente con el ocultamiento del nido

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ABSTRACT. Resource selection is a key factor influencing avian reproductive success. Nest site selection, in particular, may reduce predation risk. We studied nest site selection and daily nest survival of the Warbling Doradito (*Pseudocolopteryx flaviventris*) in relatively undisturbed natural wet grasslands of the southeastern Pampas region, Argentina. During two breeding seasons (2012 and 2013), we located and monitored nests, evaluating microhabitat vegetation characteristics and temporal variables influencing nest occurrence and survival. We used generalized linear mixed models to compare nest-supporting plant species, vegetation height, and nest visibility between nest sites and random locations. Daily nest survival rate (DSR) was estimated using logistic-exposure models incorporating microhabitat and temporal variables (year, nest age, clutch initiation date). Warbling Doraditos selected sites with shorter vegetation, more vegetation cover, and lower nest visibility, indicating a preference for concealed nest sites within structurally complex grass tussocks. Of the 47 nests monitored, 29 (62%) were depredated, 17 (36%) were successful, and one was abandoned. Mean DSR was 0.957, with a cumulative survival probability of 26.8%. Nest survival increased with greater vegetation height above the nest, likely reducing detection by aerial predators. No temporal variables affected nest survival, possibly because of structural stability of the habitat and consistent predator pressure across seasons. Our findings indicate that Warbling Doraditos select nest sites with low horizontal visibility, potentially reflecting a trade-off between concealment from terrestrial and aerial predators, consistent with patterns observed in other grassland specialists. The study underscores the importance of vegetation structure in nest site selection and survival, and highlights the conservation value of undisturbed, heterogeneous grasslands for breeding birds in the Pampas region.

RESUMEN. La selección de recursos es un factor clave que influye en el éxito reproductivo de las aves. La selección del sitio de nidificación, en particular, puede reducir el riesgo de depredación. Estudiamos la selección del sitio de nidificación y la supervivencia diaria de nidos de *Pseudocolopteryx flaviventris* en pastizales húmedos naturales relativamente poco alterados en el sudeste de la región pampeana, Argentina. Durante dos temporadas reproductivas (2012 y 2013), localizamos y monitoreamos nidos, evaluando las características de la vegetación del microhábitat y las variables temporales que influyen en la presencia y supervivencia de los nidos. Utilizamos modelos lineales generalizados mixtos para comparar las especies de plantas que sirven de soporte al nido, la altura de la vegetación, y la visibilidad del nido entre los sitios de nidificación y sitios aleatorios. La tasa de supervivencia diaria de nidos (DSR) se estimó mediante modelos de exposición logística incorporando variables de microhábitat y temporales (año, edad del nido, fecha de inicio de la puesta). *P. flaviventris* seleccionó sitios con vegetación más baja, mayor cobertura vegetal, y menor visibilidad de los nidos, lo que indica una preferencia por sitios de nidificación ocultos dentro de matas de pastos estructuralmente complejas. De los 47 nidos monitoreados, 29 (62 %) fueron depredados, 17 (36 %) tuvieron éxito y uno fue abandonado. La DSR media fue de 0,957, con una probabilidad de supervivencia acumulada del 26,8 %. La supervivencia de los nidos aumentó con la altura de la vegetación por encima del nido, lo que probablemente reduce su detección por parte de depredadores aéreos. Ninguna de las variables temporales afectó la supervivencia de los nidos, posiblemente debido a la estabilidad estructural del hábitat y a una presión de depredación constante a lo largo de las temporadas. Nuestros resultados indican que *P. flaviventris* selecciona sitios de nidificación con baja visibilidad horizontal, lo que podría reflejar un compromiso entre el ocultamiento frente a depredadores terrestres y aéreos, en concordancia con los patrones observados en otras especies especialistas de pastizales. El estudio destaca la importancia de la estructura de la vegetación en la selección del sitio de nidificación y en la supervivencia de los nidos, y pone de relieve el valor de conservación de los pastizales poco alterados y heterogéneos para las aves reproductoras de la región pampeana.

Key Words: *breeding success; grasslands; nest-site selection; nest predation; Pampas; Pseudocolopteryx flaviventris*

INTRODUCTION

Resource selection in the environment can be understood as a process by which organisms choose certain components of their surroundings more frequently than would be expected based on their availability (Manly et al. 2002). Specifically, nest site selection is one of the most important aspects of bird reproductive ecology, as it directly influences adult survival and reproductive success (Lack 1968, Martin 1993, Latif et al. 2012). This selection represents an adaptive response shaped by the evolutionary history of each species (Ricklefs 1969, Cody 1985) and is influenced by multiple ecological factors, including vegetation structure, food availability, nest support substrates, shelter, and predation risk (Martin 1993, Danchin et al. 1998, Parejo et al. 2007).

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Nest predation has been widely recognized as the main cause of reproductive failure in birds (Ricklefs 1969, Martin 1993). If habitat selection has a genetic basis, natural selection should favor individuals that choose habitats with characteristics that reduce the likelihood of nest detection by predators (Martin 1993, Martin 1998, Ibáñez-Álamo et al. 2015). Although nest site selection operates at multiple spatial scales ranging from landscape composition to local vegetation features surrounding the nest (McGarigal et al. 2016), microhabitat characteristics are particularly important because they directly determine nest concealment and accessibility to predators. At this fine spatial scale, variables such as vegetation height, density, horizontal concealment surrounding the nest, and vegetation cover above the nest may influence predation risk by reducing nest detectability by terrestrial and aerial predators (Martin 1993, Fisher and Davis 2010). Consequently, variation in vegetation structure at the nest site can strongly influence nest predation risk and reproductive success (Misenhelter and Rotenberry 2000, Fogarty et al. 2017, Colombo et al. 2024, Martin-Sirito et al. 2025; but see Johnson et al. 2012).

In passerines that nest in open habitats such as grasslands, nest height above the ground, as well as the height, density, and cover of herbaceous vegetation, play key roles in nest concealment from predators (Fisher and Davis 2010, Cardoni et al. 2012, Fogarty et al. 2017, Colombo et al. 2024). Denser or taller vegetation can hinder visual detection by predators, thereby reducing the risk of predation (Martin 1993; but see Borgmann and Conway 2015). In particular, horizontal concealment surrounding the nest and vegetation cover above the nest may reduce nest detectability by terrestrial and aerial predators, respectively (Martin 1993, Fisher and Davis 2010). Selecting nest sites with these characteristics may therefore provide an adaptive advantage (Martin 1993, 1998). However, this pattern is not entirely consistent, as several studies have shown that some species select nest site characteristics that do not necessarily reduce predation risk (Davis 2005, Perkins et al. 2013). Particularly in grazed grasslands, changes in vegetation structure associated with livestock management may alter the relationship between nest site selection and nest survival (Colombo et al. 2024, Martin-Sirito et al. 2025). These findings highlight the high variability in nest site selection strategies and their relationship with survival across species and environmental conditions, emphasizing the importance of studying grassland birds across different regions and taxonomic groups to better understand how habitat characteristics influence reproductive success.

Nest survival depends not solely on spatial location and concealment, but also on a range of temporal factors. Interannual variation in predator abundance may influence predation risk through changes in predator population dynamics, movements, or prey availability, as proposed by the alternative prey hypothesis (Pakanen et al. 2022). In addition, temporal fluctuations in food availability for breeding birds may affect parental activity and nest attendance, potentially modifying nest detectability and breeding success (Preston and Rotenberry 2006). Other factors such as the laying date (Wilson et al. 2007, Grant and Shaffer 2012) and nest age (Conkling et al. 2015, Colombo et al. 2024) may also influence nest survival, although these relationships often vary depending on ecological context.

The Pampas region of South America is one of the most extensively transformed temperate grassland ecosystems worldwide because of agricultural intensification and habitat modification, resulting in substantial alterations of vegetation structure and widespread biodiversity loss (Baldi and Paruelo 2008, Azpiroz et al. 2012). Grassland-dependent bird species are strongly affected by these changes; however, South American grasslands remain underrepresented in studies of nest site selection and nest survival, particularly at fine spatial scales (Azpiroz et al. 2012). This is especially relevant because vegetation structure directly influences predator-prey interactions and is a key determinant of reproductive success in grassland birds (Fisher and Davis 2010, Fogarty et al. 2017, Colombo et al. 2024). In particular, little is known about the reproductive ecology and nest survival patterns of the Warbling Doradito (*Pseudocolopteryx flaviventris*) in natural Pampas grasslands. Understanding the breeding ecology of this species can therefore provide valuable insights for conservation and management of grassland birds in these increasingly threatened ecosystems.

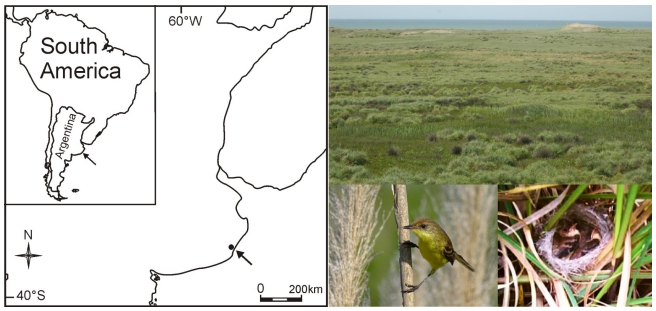
The aim of this study was to assess nest site selection and breeding success of the Warbling Doradito in natural wet grasslands of the Pampas region in Argentina. Specifically, we examined whether vegetation characteristics at the microhabitat scale predict nest occurrence, and assessed the extent to which these features, together with temporal variables, modulate nest survival. We predicted that Warbling Doraditos would preferentially select nest sites with greater concealment, characterized by lower nest visibility and vegetation structures that reduce predator detection. We also expected daily nest survival to increase with greater vegetation height and cover surrounding the nest, particularly above the nest, because these features may reduce detectability by aerial and terrestrial predators (Martin 1993, Davis 2005, Fisher and Davis 2010). We also predicted that nest survival would vary throughout the breeding season and between years because of changes in vegetation structure, food availability, and predator abundance (Grant et al. 2005, Wilson et al. 2007, Pakanen et al. 2022). Finally, we expected nest survival to decline with nest age because increased parental activity during later nesting stages may increase nest detectability by predators (Martin et al. 2000, Weidinger 2002).

METHODS

Study area and species

The study was carried out within the Parque Atlántico Mar Chiquito Biosphere reserve (37°40′ S, 57°23′ W), located on the southeastern coast of Buenos Aires Province, Argentina, within the Flooding Pampa subregion (Soriano et al. 1991). The surrounding landscape has been extensively transformed by livestock production and agriculture, whereas afforestation and urban areas occur to a lesser extent, resulting in a highly heterogeneous mosaic of land uses typical of the Pampas region (Baladrón et al. 2016). In contrast to this surrounding matrix, the reserve preserves large remnants of relatively natural wet grasslands with high structural heterogeneity, which have not been exposed to livestock grazing or recent fire events. The main natural habitats within the reserve include extensive wet grassland communities dominated by *Sporobolus densiflorus* in

Fig. 1. Location of study site (small black dot) in Parque Atlantico Mar Chiquito Biosphere Reserve, Buenos Aires province, Argentina (left). Tall grasslands of *Cortaderia selloana* dominating the upper part of the reserve (top right), and below, a female Warbling Doradito (*Pseudocolopteryx flaviventris*) and a nest with two chicks hidden in a clump of *C. selloana*.



lowland areas, grasslands dominated by *Cortaderia selloana* and *Juncus acutus* in upper zones, and interdunal lowlands dominated by *Schoenoplectus californicus*, *Solanum glaucophyllum*, and *Zizaniopsis bonariensis* (Stutz 2001, Isacch et al. 2006; Fig. 1).

The Warbling Doradito is a small (7-8 g) member of the Tyrannidae family that is present in Paraguay, southern Brazil, Uruguay, and from central to northern Argentina (Bostwick and Kirwan 2020). This species is considered resident in part of its distribution range (central Argentina: Pagano et al. 2012; southern Rio Grande do Sul: Bencke 2001; Uruguay: Azpiroz 2012). However, in our study area it is present from October to March, and once the breeding season is over, these southern populations move north again (Cardoni et al. 2016, Román and Pons 2023). The Warbling Doradito breeds from southern Brazil and Uruguay to central Argentina in reeds and flooded grasslands or near water bodies (Narosky and Salvador 1998, Cardoni et al. 2016). The nest consists of a small and compact open cup with a globular appearance fixed to grass leaves. The mean clutch ranges between 1 and 3 eggs, and the incubation period extends over approximately 17 days. Chicks remain on average 13 days in the nest (Cardoni et al. 2016). This species exhibits differential parental care investment, with females contributing more to nesting activities than males (Cardoni et al. 2017).

Nest searching and monitoring

We systematically searched for Warbling Doradito nests during two consecutive breeding seasons (October 2012–January 2013, October 2013–January 2014). We conducted non-standardized walking surveys within the reserve, using adult behavioral cues to locate breeding pairs and active nests (Winter et al. 2003). When nests were found we recorded their GPS locations and marked the nest areas with plastic tape to facilitate subsequent monitoring. We visited nests at intervals of 3 to 5 days following standard procedures to avoid attracting predators to nests (Martin and Geupel 1993). We monitored nests until they were abandoned, depredated, or produced fledglings. At each visit, we recorded egg or chick loss and the presence of adults near the nest. We considered a nest abandoned when eggs remained in the nest beyond the expected hatching date and no parental activity was detected during repeated subsequent visits, whereas nests were considered depredated when the complete clutch disappeared between two subsequent visits, or when the chicks disappeared from their nests before they were old enough to fledge. We confirmed nest success by observing fledglings or adults delivering food near the nest after it was empty and nestlings were old enough to fledge (~13 d, Cardoni et al. 2016).

Nest and habitat measures

To avoid disturbing normal nesting activity, we measured vegetation characteristics at each nest within three days after the nesting attempt had either failed or successfully fledged young. Although vegetation may have continued growing after nest construction, measurements were conducted within a short period following the end of the nesting attempt to minimize potential changes in vegetation structure. We measured the following variables associated with nest concealment: nest height from the ground (NH), measured from the ground to the base of the nest; height of vegetation above the nest (HAN), measured from the base of the nest to the higher vegetation above the nest. Specifically, we measured the following variables in the nest and at a random point within the patch where the nests were found: total height of the supporting plant (VH); nest-supporting plant (NSP); percentage cover of tall grass estimated from vegetation interception along a horizontal rod placed at 50 cm height within a 1 m radius plot centered on each nest or random point (Cov). Vegetation height variables were measured using a graduated rod marked at 1 cm intervals, positioned vertically on the ground, and recorded to the natural height of the vegetation without stretching the plant structure. The random point was selected by throwing the PVC pole (described in detail below) backward over the shoulder, and measurements were taken at the location where it landed. In addition, to assess nest visibility, we adopted a methodology similar to that proposed by Robel et al. (1970), modifying the original visual estimation approach by using photographic records to facilitate subsequent standardized assessments of horizontal nest concealment. We placed a 2 m pole (divided into twenty 10 cm segments alternating between white and black) vertically on the ground directly below each nest and at the center of each random point. Nest visibility (NV) values were obtained by averaging measurements from two photographs taken from opposite sides of each nest or random point at a distance of 4 m and a height of 1 m to capture variation in surrounding vegetation concealment, following the guidance established by Robel et al. (1970). For each segment of the pole, we visually estimated from the photographs the proportion that remained visible, with values ranging from 0% (no visibility) to 100% (fully visible). This method provided an indirect estimate of vegetation structure and density through visibility measurements (Cardoni et al. 2017, Martin-Sirito et al. 2025).

Statistical analyses

Nest site selection

We assessed nest site selection by fitting generalized linear mixed models (GLMMs) with nest identity as a random factor, a binomial error structure, and a logit link function (Crawley 2007, Zuur et al. 2009). Models included vegetation variables measured at both nesting sites and random points. We used nest presence or absence of the Warbling Doradito as the response variable (binary: 1 = presence, 0 = absence). The explanatory variables

were nest-supporting plant (NSP; factorial with three levels: *C. selloana*, *J. acutus*, *Z. bonariensis*), vegetation cover (Cov), vegetation height (VH), nest visibility (NV), all of them continuous variables. For NV variable, prior to model adjustment, we grouped the average NV values into three segments: NV_1 included all average NV values between 20 and 80 cm; NV_2 comprised values ranging from 81 to 140 cm; and NV_3 included values between 141 and 200 cm. Because Warbling Doradito nests are typically located in the lower portion of the vegetation, both according to our field observations and published descriptions of the species' nesting habits (de la Peña 2020), we considered NV_1 to be the most biologically relevant measure of horizontal nest visibility. Therefore, to simplify the analyses and focus on the vegetation stratum most directly associated with nest placement and concealment, only NV_1 was retained for subsequent analyses.

We evaluated models with information-theoretic procedures (Burnham and Anderson 2002). We considered models with all possible combinations of predictor variables. We ranked models by AICc and made comparisons between models using ΔAICc and model weights (Burnham and Anderson 2002). The AICc weight of a model (w_i) signifies the relative likelihood that the specific model is the best of the suite of all models. We calculated parameter estimates using model averaging across all candidate models, weighting estimates by their Akaike weights (w_i). We calculated 95% confidence interval limits (CL) of parameter estimates to assess the strength and direction of the effects of explanatory variables on nest site selection. Variables with confidence intervals overlapping zero were considered to have weak or inconclusive support. Statistical analyses were developed by using the statistical software R (R Core Team 2024), with packages lme4 (Bates et al. 2014) and MuMin (Burnham and Anderson 2002). In all cases, model fit was evaluated by examining simulated residuals using the DHARMa package (Hartig 2024), and no major deviations from model assumptions were detected.

Nest survival

We estimated the daily nest survival rate (DSR) using generalized linear models with a logistic-exposure link function (Shaffer 2004). These models include the duration of each visit interval as exposure time (in days) and the fate of the nest as the response variable (coded as 0 = failed during the interval and 1 = survived the interval). We created an intercept-only model of constant DSR to estimate the cumulative nest survival probability for the species by raising the DSR to a power equal to the length (in days) of a complete breeding cycle. Cumulative nest survival probability was estimated over a complete breeding cycle of 30 days (17 days for the egg-laying and incubation stages, and 13 days for the nestling stage; Cardoni et al. 2016). We assigned a clutch-initiation date to each nest corresponding to the date of laying of the first egg. We were able to determine clutch-initiation dates for nests found during construction and egg-laying (n = 19 nests). Clutch-initiation dates were assigned by backdating from hatching dates (n = 23 nests) for nests found during incubation, and, for nests found after hatching (n = 5 nests), by using nestling weights (Cardoni et al. 2016). For two nests that failed during incubation, we estimated clutch-initiation dates by assuming that the observed period was halfway between the end of laying (nest age 2) and hatching (nest age 17; e.g., if a nest was observed for 4 days, we considered that it was observed between nest ages 8 and 11; if it was observed for 6 days, we considered that it was observed between nest ages 7 and 12).

Table 1. Description of variables considered for the Warbling Doradito (*Pseudocolopteryx flaviventris*) nest site selection and nest survival models in Mar Chiquita Biosphere Reserve, Argentina.

Variable	Description	Nest site selection	Survival
Age	Nest age since start of egg laying		x
Date	Time of clutch initiation within season		x
Year	Field season of each nest (2012–2013, 2013–2014)		x
NV	Nest visibility measured in 10-cm height categories from 20 to 80 cm (NV_1).	x	x
Cov	Amount (%) of tall grass cover in a 1 m-radius plot around a nest	x	x
NH	Nest height from the ground		x
HAN	Height of vegetation above the nest		x
NSP	Nest-supporting plant (*Cortaderia selloana*, *Juncus acutus*, and *Zizaniopsis bonariensis*)	x	x
VH	Vegetation height (total height of the supporting plant)	x	

To assemble the set of candidate models, we applied a stepwise method aimed at minimizing redundancy among models subjected to evaluation (Arnold 2010). In the first phase, we investigated the possible effects of temporal factors that could, based on prior knowledge, influence nest survival. These factors included the year, the clutch initiation date (expressed as the ordinal day of the year), and nest age (measured as the number of days elapsed since the first egg was laid) (Grant et al. 2006, Colombo et al. 2024). Furthermore, to determine habitat variables affecting nest DSR, we developed an additional set of candidate models incorporating explanatory variables selected on the basis of factors presumed a priori to impact nest survival (see Table 1). We used Spearman's rank correlation coefficient to control for correlation among continuous nesting habitat variables. These models were ranked according to their AICc values, and the variables present in the best model were kept for the following stage. We built a final model set including the variables present in the best models of each step and all of the possible combinations among them. We evaluated the final model set based on AICc values following the same criteria as for nest site selection. We calculated parameter estimates using model averaging across all models included in the final candidate model set, weighting estimates by their Akaike weights (w_i). Parameters were considered informative when their 95% confidence intervals did not include zero. We conducted nest survival analyses using software R (R Development Core Team 2024), package MASS (Venables and Ripley 2002).

RESULTS

We found 47 nests over the two breeding seasons (24 in 2012–2013 and 23 in 2013–2014). We monitored nests at the reserve over 68 days (2 November–8 January) for a total of 759 exposure days, during which 17 (36%) nests were successful, 29 (62%) were depredated, and only one (2%) was abandoned. Thirty-six nests were located in *C. selloana*, 7 in *Z. bonariensis*, and 4 in *J. acutus*. Thirteen nests were found during construction, 6 during the egg-

Table 2. Candidate generalized linear mixed models (GLMMs) explaining nest site selection of the Warbling Doradito in Mar Chiquita Biosphere Reserve (Argentina), ranked by support based on Akaike's Information Criterion corrected for small sample sizes (AICc). *k* denotes the number of estimated parameters, ΔAICc the difference in AICc relative to the top-ranked model, and w_i the Akaike weight representing the relative support for each model. Explanatory variables included VH, vegetation height; NV1, nest visibility; Cov, amount (%) of tall grass cover; and NSP, nest-supporting plant.

Model	*k*	ΔAICc	w_i
VH + Cov + NV_1	5	0.00	0.899
VH + Cov + NV_1 + NSP	7	4.63	0.089
VH + NV_1	4	9.32	0.009
VH + NSP + NV_1	6	11.35	0.003

Best supported model AICc = 63.0.

laying period, 23 during incubation, and 5 after chicks had hatched. The average number of fledglings per successful nest was 2.18 ± 0.89 (mode = 2, range = 1–3 fledglings, *n* = 17 nests).

Nest site selection

Model selection for nest site selection by the Warbling Doradito indicated that the model including vegetation height, vegetation cover, and nest visibility received the strongest support (Table 2). To account for model selection uncertainty, we based inference on model-averaged parameter estimates. Model-averaged results showed that vegetation height, vegetation cover, and nest visibility had 95% confidence intervals that did not overlap zero, indicating strong support for their effects (Table 3). These results indicate that the Warbling Doradito selected nest sites where vegetation was shorter, the amount of tall grass cover was higher, and nest visibility was lower than at random sites (Fig. 2).

Nest survival

We estimated a daily survival rate of 0.957 ± 0.007 (SE) from the intercept-only model based on 47 nests, resulting in an estimated cumulative survival probability of 0.268 ± 0.065 (SE) over the average nesting period. Nest age and breeding season were the temporal variables that best explained DSR, whereas nest height above the ground and vegetation height above the nest were the habitat variables receiving the strongest support (Table 4). The top-ranked model from the final set indicated an increase in DSR as vegetation height above the nest increased (Table 5, Fig. 3). Although nest age and breeding season were also included in the best model, showing a trend toward increasing DSR with nest age and higher nest survival during the second breeding season (see Table 5), the 95% confidence intervals for these effects included zero, suggesting weak support for these relationships.

DISCUSSION

In this study, we present novel information on the reproductive ecology of the Warbling Doradito, identifying the factors involved in nest site selection and assessing the potential role of microhabitat and temporal variables in shaping daily nest survival rates in natural wet grasslands of the Pampas region, Argentina. The Warbling Doradito exhibited non-random patterns of nest site selection, with vegetation structure emerging as a relevant factor. Nest occurrence was influenced by total vegetation height and concealment, whereas the height of vegetation above the nest affected nest survival. However, we found no effects of the temporal variables evaluated on nest survival.

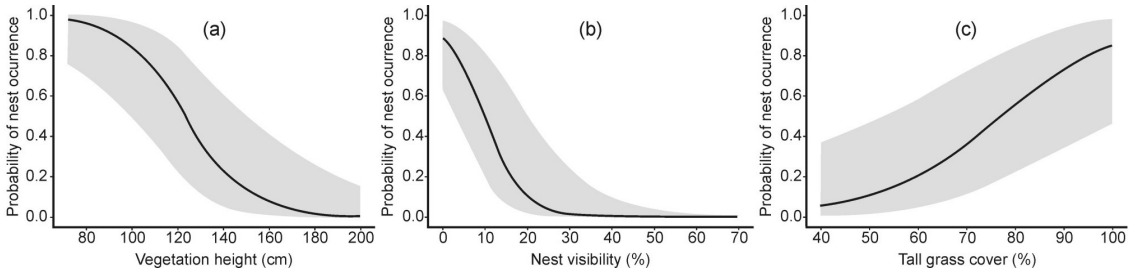
Table 3. Model-averaged parameter estimates (β), SE (standard error) and 95% confidence interval limits (CI) explaining nest site selection of the Warbling Doradito in Mar Chiquita Biosphere Reserve, Argentina. VH, vegetation height; NV1, nest visibility; Cov, amount (%) of tall grass cover; and NSP, nest-supporting plant. Coefficients are based on model averaging across the candidate set. Variables whose 95% CI did not overlap zero are shown in bold and were considered informative predictors of nest site selection.

Explanatory variable	Parameter estimate (β)	SE	95% CI	
			Lower	Upper
(Intercept)	5.066	3.150	−1.205	11.338
VH	**−0.072**	**0.022**	**−0.117**	**−0.026**
NV_1	**−0.210**	**0.055**	**−0.321**	**−0.099**
Cov	**0.075**	**0.027**	**0.024**	**0.128**
NSP				
Cortaderia selloana	−0.055	0.552	−4.014	2.844
Juncus acutus	−0.006	0.371	−2.512	2.361
Zizaniopsis bonariensis	0.055	0.552	−2.844	4.041

The natural wet grassland at the study site comprises a heterogeneous mosaic of plant communities (Isacch et al. 2006), resulting in a high degree of heterogeneity in vegetation structure. Nearly all nests included in our analyses were found in only three plant species (*C. selloana*, *J. acutus*, and *Z. bonariensis*). A few additional nests were observed in *S. glaucophyllum* during fieldwork, but these were excluded from the analyses because of their low sample size. Although we did not quantify the availability of potential nesting substrates and therefore cannot infer plant species selection, these three species share structural characteristics that likely provide adequate support and sufficient vertical and horizontal concealment for nesting. Other common grasses present in the reserve, such as *Festuca arundinacea* and *S. densiflorus*, generally develop shorter and less complex vegetation structures, potentially providing less suitable nesting conditions. Notably, all nests observed in *S. glaucophyllum* occurred only within dense patches associated with other tall emergent plants, particularly *S. californicus*. These observations suggest that nest site selection may be more closely associated with vegetation structure than with particular plant species, highlighting the importance of the surrounding vegetation context in determining nest site suitability.

Because of the absence of grazing in the reserve, taller grass species such as *C. selloana* can reach heights of up to 2 m. Within this vertical variation, Warbling Doraditos tended to nest in relatively lower growing grass tussocks (range = 10–76 cm). Furthermore, this choice was associated with vegetation structure and tall grass cover that enhances nest concealment, suggesting that nest site selection prioritizes conditions that maximize cover and protection against potential predators (Davis 2005, Frey et al. 2008). Our results are consistent with findings for other sympatric nesting passerines, such as the Spectacled Tyrant (*Hymenops perspicillatus*), known to prioritize nest concealment during nest site selection in

Fig. 2. Predicted probability of nest occurrence of the Warbling Doradito in the Mar Chiquita Biosphere Reserve, Buenos Aires Province, Argentina, according to (a) vegetation height (VH), (b) nest visibility (NV), and (c) tall grass cover (Cov). Predictions were obtained from model-averaged coefficients based on all models included in the final model set. For each plot, the focal variable was allowed to vary across its observed range while the remaining continuous predictors were held at their mean values and vegetation type was fixed at the reference category (*Cortaderia selloana*). Shaded areas represent the 95% confidence intervals.



both natural and grazed grasslands (Martin-Sirito et al. 2025), and the Grassland Yellow-Finch (*Sicalis luteola*), which maximizes nest concealment both laterally and above the nest (Colombo et al. 2024, Martin-Sirito et al. 2025). In the latter species, nest sites tend to be located in vegetation taller than expected by chance (Colombo et al. 2024), likely reflecting differences in the prevailing vegetation structure. Together, these findings suggest that nest height selection is context-dependent, with species adjusting nest placement relative to local vegetation height to maximize concealment and protection. In particular, nest placement within the grass tussock reflects a trade-off between the risk of predation from the ground by small mammals and from above by birds, with nests placed at intermediate heights (mean = 41.6 cm) generally exhibiting higher survival rates (Cardoni et al. 2012, Kleindorfer et al. 2021).

The breeding success of the Warbling Doradito (26.8%) was lower compared to that of the Spectacled Tyrant (46.7%) and the Brown-and-yellow Marshbird (*Pseudoleistes virescens*; 52.6%), all nesting in natural wet grasslands at the same study site (Pretelli et al. 2015). However, it was higher than the values recorded for the Grassland Yellow-Finch (16.9%), Grassland Sparrow (*Ammodramus humeralis*; 11%), and Hellmayr's Pipit (*Anthus hellmayri*; 7.4%), species that also breed in the Pampas region. For the latter three species, nests were located in grazed fields, which may be associated with their lower breeding success rates (Colombo et al. 2021, 2023, 2024).

Warbling Doraditos actively selected nest sites with lower horizontal visibility, indicating a preference for greater concealment than expected by chance. However, horizontal visibility did not directly influence nest survival. This pattern suggests that the species appears to avoid highly exposed nest sites during nest placement, thereby restricting the range of horizontal visibility conditions represented among observed nests. As a result, variation in horizontal concealment among nest sites may have been insufficient to produce detectable differences in nest survival. This interpretation is consistent with the "adaptive peak hypothesis," which proposes that adaptive nest site selection can reduce the observable relationship between habitat features and nest survival because individuals preferentially occupy safer microhabitats (Latif et al. 2012). In contrast, greater vegetation height above the nest was associated with a lower probability of predation, likely because this feature varies more widely within the study system. Increased vegetation height above the nest may reduce detectability by aerial predators such as the Chimango Caracara (*Daptrius chimango*) and the Long-winged Harrier (*Circus buffoni*), both common in the area (Pretelli et al. 2023), potentially reducing predation rates (Colombelli-Négrel and Kleindorfer 2009, Dinkins et al. 2016). Despite the availability of tall grasses in the study area, Warbling Doraditos consistently nested in shorter grass tussocks. As a result, their nests may not fully benefit from vegetation cover above the nest, potentially increasing detectability by aerial predators, whereas horizontal concealment may be less effective against these predators. This interpretation is consistent with findings in the Grassland Yellow-Finch, in which vegetation cover above the nest was positively associated with nest survival, whereas horizontal concealment had no significant effect (Colombo et al. 2024).

Although the temporal variables year and nest age were included in the top-ranked model, they did not have effects on daily nest survival. Model selection uncertainty was relatively high, as several competing models received similar support (Table 4). Nevertheless, vegetation height above the nest (HAN) was consistently retained among the best supported models, reinforcing its potential importance in reducing aerial detectability and predation risk in this species. This result contrasts with findings from other studies where both variables frequently influence nest survival due to changes in parental activity (Grant et al. 2005, Conrey et al. 2016, Colombo et al. 2024) and predator abundance (Sherry et al. 2015). However, the absence of these temporal effects has also been reported in other bird species (Chapa-Vargas and Robinson 2007, Gorosito 2020, Colombo et al. 2021). At our study site, the absence of interannual variation in nest survival could be explained by the structural stability of the sampled natural grassland, characterized by dense vegetation throughout both study seasons. Unlike managed grasslands where vegetation structure is strongly influenced by grazing or fire, these wet grasslands are maintained by hydrological processes, including recurrent flooding driven by rainfall and tidal dynamics, which limit woody plant encroachment and promote the persistence of dense herbaceous communities. This environment stability may have buffered phenological changes that, in other systems, cause variations in

Table 4. Candidate logistic-exposure models explaining daily survival rates (DSR) of Warbling Doradito nests (n = 47) in the Mar Chiquita Biosphere Reserve, Argentina. Explanatory variables included HAN, vegetation height above the nest; NH, nest height above ground; NV, nest visibility; Cov, percentage of tall grass cover; NSP, nest-supporting plant; Year, breeding season; Age, nest age since the start of egg laying; and Date, timing of clutch initiation within the breeding season. k is the number of estimated parameters; ΔAICc is the difference in Akaike's Information Criterion corrected for small sample sizes relative to the best-supported model; and w_i is the Akaike weight representing the relative support for each model. Variables retained in the best-supported models from the preliminary model subsets were combined to construct the final candidate model set. Models are ranked according to ΔAICc, and only models with ΔAICc < 3 are shown.

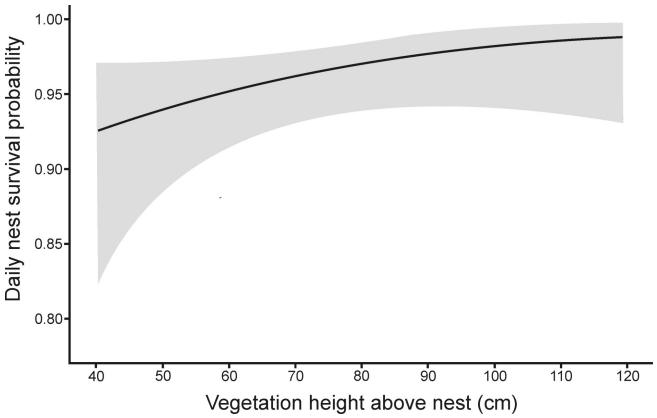
Models	k	ΔAICc	w_i
Time-specific variables			
Age + Year	3	0.00	0.305
Year	2	0.71	0.214
Age	2	1.57	0.139
Age + Date + Year	4	1.95	0.115
Date + Year	3	2.73	0.078
Age + Date	3	2.99	0.068
Nesting habitat variables			
NH + HAN	3	0.00	0.176
HAN	2	0.13	0.165
HAN + NV	3	0.84	0.116
HAN + Cov	3	1.82	0.071
HAN + NH + NV	4	1.87	0.069
HAN + NH + Cov	4	2.04	0.064
HAN + NSP	4	2.63	0.047
HAN + Cov + NV	4	2.78	0.044
Final model set			
HAN + Age + Year	4	0.00	0.199
HAN + Year	3	0.29	0.172
HAN + Age	3	1.04	0.118
HAN + NH + Age	4	1.78	0.082
HAN + NH + Age + Year	5	2.03	0.072
HAN + NH	3	2.10	0.070
HAN + NH + Year	4	2.14	0.068
HAN	2	2.23	0.065

Best supported model AICc values for each model set were: 165.0 for time-specific variables, 163.8 for nesting habitat variables, and 161.7 for the final model set.

Table 5. Model-averaged parameter estimates (β), SE (standard error) and 95% confidence interval limits (CI) explaining daily survival rates of Warbling Doradito nests in Mar Chiquita Biosphere Reserve, Argentina. NH, nest height from the ground; Year, field season of each nest; and Age, nest age since start of egg laying. Coefficients are based on model averaging across all models included in the final model set. Variables whose 95% CI did not overlap zero are shown in bold and were considered informative predictors of nest survival.

Explanatory variable	Parameter estimate (β)	SE	95% CI	
			Lower	Upper
(Intercept)	1.191	1.300	−1.369	3.751
HAN	**0.028**	**0.013**	**0.001**	**0.054**
NH	−0.013	0.016	−0.046	0.019
$Year_2$	0.709	0.416	−0.112	1.532
Age	0.039	0.024	−0.009	0.089

Fig. 3. Predicted probability of daily nest survival of the Warbling Doradito in the Mar Chiquita Biosphere Reserve, Buenos Aires Province, Argentina, as a function of vegetation height above the nest (HAN). Predictions were obtained from model-averaged coefficients derived from all models included in the final model set. Nest age (Age) and nest height above ground (NH) were held at their mean values, and predictions were averaged across breeding seasons (2012–2013 and 2013–2014). Shaded area represents the 95% confidence intervals.



nest visibility or predation pressure, thereby reducing the influence of year on nest survival. Alternatively, the lack of interannual variation in nest survival could also be due to a relatively constant predator abundance across years (Martin 1993, Schmidt and Ostfeld 2003), or to the short duration of this study (only two breeding seasons), which may have been insufficient to detect real fluctuations in nest survival (Lloyd and Martin 2005). Future studies incorporating direct estimates of predator abundance across years may help to clarify the influence of temporal variation in predation risk on nest survival.

Nest age did not affect survival in the Warbling Doradito, which is consistent with findings reported for several species within the Tyrannidae family (Mezquida and Marone 2001, Marini et al. 2009, Anciães et al. 2012, Gorosito 2020). In general, increased parental activity associated with higher provisioning needs can elevate the risk of predation (Martin et al. 2000, Weidinger 2002). However, this increased predation risk may be partially offset by intensified parental defense behaviors, such as alarm calls, distraction flights, or direct attacks on predators (Montgomerie and Weatherhead 1988, Ghalambor and Martin 2000). In particular, we have documented Warbling Doraditos actively defending their nests by repelling avian predators such as the Freckle-breasted Thornbird (*Phacellodomus striaticollis*) (Pretelli et al. 2023), which may have mitigated an increase in predation risk during later nesting stages. Nevertheless, some methodological aspects may also have contributed to the absence of temporal effects detected in our models. Although nest age was incorporated as a continuous temporal covariate, potentially capturing variation across nesting stages, differences in parental

activity between incubation and nestling stages may still influence nest detectability and predation risk. In addition, because the logistic-exposure approach estimates covariate effects across monitoring intervals (Shaffer 2004), rapid temporal changes occurring between nest visits may have reduced our ability to detect fine-scale temporal effects on nest survival.

In summary, our results highlight the importance of grassland structure in the breeding ecology of the Warbling Doradito, influencing both nest site selection and nest survival. The positive association between vegetation height above the nest and nest survival suggests that reduced aerial visibility may play an important role in shaping predation risk. These findings not only provide novel information on a poorly studied species, but also underscore the importance of conserving grasslands with high structural complexity to support the breeding success of specialist birds. In the Pampas region, ongoing agricultural intensification, livestock management, and urbanization have substantially modified vegetation structure and reduced the extent of natural grasslands, potentially affecting nest concealment and predator-prey interactions. Consequently, remaining natural grassland remnants such as those preserved within protected areas may play an important role in maintaining suitable breeding habitat for grassland birds.

Author Contributions:

Matías Pretelli: Conceptualization, Investigation, Formal analysis, Writing – original draft, Writing – review & editing. Alejandro Baladrón: Investigation, Writing – review & editing. Matilde Cavalli: Conceptualization, Formal analysis, Writing – review & editing. Stella B. Román: Data curation, Writing – review & editing. Augusto Cardoni: Methodology, Investigation, Funding acquisition, Writing – review & editing. Juan P. Isacch: Investigation, Writing – review & editing.

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Data Availability:

Data supporting the findings of this study are available upon reasonable request.

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