

Variation in mesopredator abundance and nest predation rate of the endangered Strange-tailed Tyrant *Alectrurus risora*

MELANIE BROWNE,^{1*} CONSTANZA PASIAN,¹ ALEJANDRO G. DI GIACOMO,² MARIO S. DI BITETTI,^{3,4,5} & ADRIÁN S. DI GIACOMO¹

¹ *Laboratorio de Biología de la Conservación, Centro de Ecología Aplicada del Litoral (CECOAL-CONICET), Corrientes, Argentina*

² *Departamento de Conservación, Aves Argentinas/Asociación Ornitológica del Plata, Matheu 1246, C1249AAB Buenos Aires, Argentina*

³ *Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Bertoni 85, Puerto Iguazú, Misiones, Argentina*

⁴ *Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Bertoni 85, Puerto Iguazú, Misiones, Argentina*

⁵ *Facultad de Ciencias Forestales, UNaM, Bertoni 124, Eldorado, Misiones, Argentina*

* Corresponding author.

Email: melaniebrowne.mb@gmail.com

We thank the Administración de Parques Nacionales, the Dirección de Parques y Reservas de Corrientes, and the Dirección de Recursos Naturales for granting us permission to work in Iberá National Park (permit number: IF-2018-53280705-APN-DRNEA#APNAC) and Alparamis S.A. and Aves Argentinas for allowing us to work in Reserva El Bagual. We also thank A.C. Giese for her help in data analysis, M.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1111/ibi.13202](https://doi.org/10.1111/ibi.13202)

Accepted Article

Álvarez Correa, D.G. Barcos, F. Bres, C. Bruzzese, B. Cortés, H.H. Correa, A.B. Fariña, N.V. Got, A. Moreira, G. Reyes Benz, F. Sánchez Gavier, and F. N. Zarza for their assistance in the field and the Associate Editor, Alexandre Millon, and two anonymous reviewers for providing many helpful comments to improve the manuscript.

Funding Statement: This study was supported by grants from the Neotropical Grassland Conservancy, the Neotropical Bird Club, the Association of Field Ornithologists, the American Society of Mammalogists, Agencia Nacional de Promoción Científica y Tecnológica [PICT 2014-3397, PICT 2018-3407], and CONICET [PUE 229 20180100001 CO]. The funding sources had no involvement in study design, data collection, analysis, and interpretation, writing of the manuscript, nor in the decision to submit the article for publication.

Author Contributions: M.B.: Formal analysis, Methodology, Investigation, Data curation, Funding acquisition, Writing – Original Draft, Visualization. C.P.: Methodology, Data curation, Investigation, Funding acquisition, Writing – Review & Editing. A.G.D.G: Data curation, Investigation, Resources. M.S.D.B.: Methodology, Conceptualization, Resources, Writing – Review & Editing. A.S.D.G.: Methodology, Conceptualization, Supervision, Writing – Original Draft, Project administration, Funding acquisition.

Data availability statement: All scripts and files needed to reproduce our analyses will be archived in Mendeley Data upon acceptance.

Running head: *Strange-tailed Tyrant nest predation*

Variation in mesopredator abundance and nest predation rate of the endangered Strange-tailed Tyrant (*Alectrurus risora*)

MELANIE BROWNE,^{1*} CONSTANZA PASIAN,¹ ALEJANDRO G. DI GIACOMO,² MARIO S. DI BITETTI,^{3,4,5} & ADRIÁN S. DI GIACOMO¹

¹ *Laboratorio de Biología de la Conservación, Centro de Ecología Aplicada del Litoral (CECOAL-CONICET), Corrientes, Argentina*

² *Departamento de Conservación, Aves Argentinas/Asociación Ornitológica del Plata, Matheu 1246, C1249AAB Buenos Aires, Argentina*

³ *Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Bertoni 85, Puerto Iguazú, Misiones, Argentina*

⁴ *Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Bertoni 85, Puerto Iguazú, Misiones, Argentina*

⁵ *Facultad de Ciencias Forestales, UNaM, Bertoni 124, Eldorado, Misiones, Argentina*

* Corresponding author.

Email: melaniebrowne.mb@gmail.com

ABSTRACT

Nest predation is the main cause of nest failure in passerine birds and thus a key determinant of breeding traits. Accordingly, nest predator community composition and abundance modulate nest predation rates. When top predators are absent, mesopredator populations may become unchecked which in turn increases the predation pressure on their prey species. We evaluated whether nest predator abundance and breeding traits of an endangered grassland bird, the

Strange-tailed Tyrant *Alectrurus risora*, differed between two protected areas: Iberá National Park (INP), where top predators have been extinct for 50 years, and Reserva El Bagual (REB), where Pumas *Puma concolor* still have a stable population. We measured abundances of potential nest predator species and during the 2015–2018 breeding seasons we monitored Strange-tailed Tyrant nests and set camera traps to identify nest predators. Mesopredator abundance was higher in INP, and foxes were identified as the main nest predators. Nest predation rate was also higher in INP, where the daily nest predation rate and cumulative probability of nest predation were 0.05 ± 0.006 and 0.81, while in REB they were 0.04 ± 0.004 and 0.70, respectively. The 10-times higher frequency of fox records in INP could explain the higher nest predation rate observed, suggesting that the extinction of top predators may increase nest predation rates of endangered grassland birds in protected areas through release of native mesopredator species. The lower nest predation observed in REB was compensated by a higher nest abandonment rate which resulted in a similar fledgling production in the two study sites. Clutch size, hatching success and number of nestlings did not differ between study sites. The low breeding success recorded for this endangered species despite its populations being in protected areas of high conservation value is alarming given the global decline grassland bird populations are facing.

Keywords: breeding biology, camera trap, mesopredator release, nest concealment, nest predators, subtropical grasslands

INTRODUCTION

Habitat loss is one of the main drivers of biodiversity decline, and grasslands are among the most

imperilled ecosystems due to their alarming loss and degradation rates (Hoekstra *et al.* 2005, Watson *et al.* 2016). As a result, grassland birds are suffering worldwide negative population trends (Azpiroz *et al.* 2012). Subtropical grasslands are among the ecosystems that suffer the highest rates of habitat conversion and, in consequence, 22 bird species of south-eastern South American grasslands are globally threatened or near-threatened with extinction (Azpiroz *et al.* 2012, Watson *et al.* 2016).

The main cause of nest failure in many passerine birds is nest predation, making it a key modulator of avian life history traits (Ricklefs 1969, Martin 1995). Birds seek to minimize the risk of nest failure by selecting both nest sites that are concealed from potential predators and nest substrates that impede predation (Martin & Roper 1988, Schmidt & Whelan 1999, Misenhelter & Rotenberry 2000). Nest predation probability may also increase with nest age, as increasing adult and nestling activity risk betraying the nest position to potential predators (Skutch 1949). Thus, birds may respond to an increase in nest predation risk by switching their nest-site choice in favour of better concealed sites and regulating their behaviour by reducing activity at the nest (Skutch 1949, Fontaine & Martin 2006, Zanette *et al.* 2011). Breeding traits such as clutch size and fledgling production can also be reduced by an increase in nest predation risk (Zanette *et al.* 2011, Dillon & Conway 2018). The influence of nest predation on annual breeding success is conditioned by breeding season length and renesting intervals which determine the number of breeding attempts (Roper *et al.* 2010). Nest predation may thus regulate multiple breeding traits of birds.

Nest predation is also modulated by nest predator community composition and predator abundance (Schmidt *et al.* 2003, Roos *et al.* 2008). Habitat fragmentation, the extinction or suppression of top predators and the introduction of exotic species may increase nest predator

Accepted Article

densities (Roos *et al.* 2008, Saggiomo *et al.* 2021). The mesopredator release hypothesis states that the decline or extinction of top predator populations may trigger an increase in mesopredator abundance (Soulé *et al.* 1988, Crooks & Soulé 1999). As mesopredator abundance increases, the predation rate on their prey is also expected to increase. For example, mesopredator release has been reported to negatively impact bird populations, sometimes even leading to local extinctions (Soulé *et al.* 1988, Crooks & Soulé 1999, Schmidt 2003, Rees *et al.* 2019, Jiménez *et al.* 2019), through increasing nest predation rates and reducing breeding success (Rogers & Caro 1998, Ritchie & Johnson 2009, Ortega *et al.* 2021).

North-eastern Argentina's grasslands are being transformed by intensification of cattle grazing and afforestation (Viglizzo *et al.* 2011, Azpiroz *et al.* 2012). In addition, Jaguars *Panthera onca* and Pumas *Puma concolor* have been the subject of persecution due to conflict with livestock management, resulting in the extinction of the former and a population reduction of the latter in north-eastern Argentina's grasslands (Graham *et al.* 2005, Quiroga *et al.* 2014, Di Bitetti *et al.* 2016, Quiroga *et al.* 2016). Simultaneously, the Strange-tailed Tyrant *Alectrurus risora*, an endemic grassland species which nests in tallgrass tussocks and occurs primarily in north-eastern Argentina and south-eastern Paraguay, has suffered an estimated 90% reduction in its range in Argentina (Di Giacomo & Di Giacomo 2004, Di Giacomo *et al.* 2011). This drastic range reduction and the threat habitat conversion poses for its remaining natural habitat has led the species to be categorized as globally Vulnerable (BirdLife International 2016).

The main goal of this study was to evaluate if differences in the breeding biology of the Strange-tailed Tyrant in grasslands of high conservation value are associated with differences in predator abundance and predation rate. Given that one of our study sites has a stable Puma population but top predators are locally extinct in the other area, we studied the nest predator

community to evaluate whether nest predator abundance increased where top predators were absent and whether this variation in nest predator abundance could be associated with differences in this bird's breeding biology. We first evaluated differences in the abundance of potential nest predators, including carnivorous mammals, raptors and snakes, in both study areas. Next, we compared the breeding biology of the Strange-tailed Tyrant in the two areas, in order to determine whether its breeding phenology, breeding parameters (i.e. clutch size, hatching success, number of nestlings and fledgling production), nest predation rate, daily nest survival rate and nest concealment differed between them. We predicted a higher abundance of mesopredators with negative effects on the breeding biology of the Strange-tailed Tyrant in the study area where top predators are extinct.

METHODS

Study Area

The study was conducted in Portal San Nicolás (28.1282°S, 57.4346°W; 16,780 ha) in Iberá National Park (INP), located in the province of Corrientes, and in Reserva El Bagual (REB; 28.1869°S, 58.8550°W; 3,300 ha), located in the province of Formosa, Argentina (Fig. 1). Jaguars have been extinct in Corrientes for over 50 years and Pumas are mostly absent or extremely rare while, in Formosa, Puma populations are still stable and Jaguars, even though rare, are also present (Di Giacomo & Krapovickas 2005, Quiroga *et al.* 2014, Di Bitteti *et al.* 2016, Quiroga *et al.* 2016). Both protected areas are in the humid Chaco ecoregion (Oyarzabal *et al.* 2018). The landscapes of the study areas are physiognomically similar and consist of open savannas with gradual slopes that result in seasonally flooded grasslands in the lowlands and

drained grasslands in the uplands. Uplands are dominated by *Andropogon lateralis* in INP, and by *Imperata brasiliensis* and *A. lateralis* in REB (Carnevali 1994, Di Giacomo & Krapovickas 2005). Lowlands are dominated by *Paspalum durifolium* in INP and by *Paspalum intermedium* and *Sorghastrum setosum* in REB (Carnevali 1994, Di Giacomo & Krapovickas 2005). Both study sites support stable Strange-tailed Tyrant populations.

Nest predator surveys

We surveyed the occurrence of mammals, raptors and snakes in both study sites. To evaluate medium and large-sized mammal occurrences (O'Connell *et al.* 2011), we set 27 camera-trap stations in each study area between March and July 2015, with a minimum nearest-camera distance of 800 m. The mammal abundance survey did not coincide with the Strange-tailed Tyrant breeding season as the camera-traps were used during that period to detect nest predators (see below). Even though we did not conduct the mammal survey during the study species' breeding season, we considered the data likely to be representative of mammal abundance throughout the year as we used scented bait to attract predators and thus eliminated possible daily activity pattern differences and we have no evidence of strong interannual or seasonal fluctuations of medium and large-sized mammal populations at our study sites. We used Reconyx HyperFire HC500 cameras baited with perforated tuna cans to attract carnivorous species, as described by Di Bitetti *et al.* (2009). Cameras were set to take three pictures per trigger, with a picture interval of one second and a quiet period of three minutes. We replaced bait, batteries and memory cards every 10 days. Cameras were simultaneously active in both sites and sampling was divided in two stages, with half of the stations active during March–April and the other half during May–June.

We conducted raptor surveys during the 2017 Strange-tailed Tyrant breeding season by fixing six and two 1-km long transects across internal roads in INP and REB, respectively (Ralph *et al.* 1993). Transects were separated by a minimum distance of 500 m. We visited each transect on four occasions at both sites and recorded all raptor species and number of individuals observed within a radius of 100 m from the observer.

We sampled snakes by setting six array traps in each study site, during the 2017 breeding season. We built array traps following the design proposed by Leynaud and Bucher (2005) with 8m long legs. Array traps were separated by a minimum distance of 600 m. The traps were active in both sites for 42 consecutive days, and we conducted daily visits to check for contents, identify captured individuals, and immediately release them.

We only included in the analysis mammals of the order Carnivora (the only order with confirmed nest predators), and raptor and snake species that were confirmed to be potential nest predators either during our study (i.e. we registered a predation event) or by bibliographical references on nest predators of Neotropical grassland birds (Di Giacomo & Krapovickas 2005, Menezes & Marini 2017), hereafter referred to as mammals, raptors or snakes. Four camera-trap stations suffered technical problems and were discarded from the analyses, resulting in 26 stations in INP and 24 in REB. Sampling effort was 1686 camera-trap days in INP and 1834 camera-trap days in REB. We identified photographed mammals to species level and considered records of the same species as independent if > 12 h elapsed between successive pictures. We computed the frequency of mammal records as the number of records per station divided by the number of days the station was active (Di Bitetti *et al.* 2009).

Nest searches and monitoring

We conducted searches for Strange-tailed Tyrant nests during four consecutive breeding seasons in September - December 2015 - 2018. In both protected areas we concentrated searches in grassland patches of ~60 ha. We found and monitored 270 nests (98 in INP, 172 in REB). The study species is sexually dimorphic and has a socially polygynous mating system (Di Giacomo *et al.* 2011). We identified territories by observing the flight displays of males and then focused on female behavioural cues for nest searches as only females construct the nest, incubate and provision nestlings (Di Giacomo *et al.* 2011). We located nests during the nest building, incubation or building stages and georeferenced them with a Garmin GPS device (Garmin International, Olathe, Kansas, USA). We checked nest contents every two to four days (i.e. we concentrated nest visits near to hatching and fledgling dates) until nest fate was determined (Martin & Geupel 1993). When nest activity concluded, we identified the nest substrate species.

We set Reconyx HyperFire HC500 camera traps (Reconyx, Holmen, Wisconsin, USA), previously cleaned with alcohol to reduce human scent, during both the incubation and nestling periods, at a minimum distance of one metre from the nest to identify nest predators. We monitored 71 nests in INP and 29 nests in REB. Camera traps were programmed to take three pictures per trigger, with a picture interval of one second and no quiet period.

Nest concealment

We measured nest concealment of 39 nests in INP and 29 nests in REB by photographing 13 cm wide discs (i.e. the maximum outer diameter of nests) in 2017 and 2018. Discs consisted of a grid of 1 cm² squares and were placed above the nest and on its side to determine overhead and lateral nest concealment, respectively (Davis 2005). We took photographs of the discs at 1 m from the nest in both orientations (Supporting Information Fig. S1). If the position of the nest

was altered by the predator, we did not take photographs. We estimated nest concealment as $1-p$ (where p = the proportion of exposed squares) such that well-concealed nests received the highest scores (Davis 2005).

Breeding parameters

We defined clutch size as the number of eggs laid, discarding nests that were predated or abandoned before laying was completed. We assessed hatching success only for nests that were found during incubation, survived until the nestling phase and for which the number of chicks remained constant on two consecutive visits. We estimated fledgling production as the number of chicks that successfully fledged per nest (i.e. per breeding attempt) considering both successful and unsuccessful nests.

Statistical analysis

Potential nest predator frequency of records

To compare mammal frequency of records between study sites, we used zero-inflated generalized linear models (GLM) with Gamma distribution when a mammal species was recorded in both study sites. Zero-inflated models comprise a zero-inflation model that describes the probability of observing an extra zero that is not generated by the conditional model using a logit link function, and a conditional model that describes the frequency observed using a Gamma distribution with an inverse link function. In this way, the zero-inflated model indicates whether the species had a higher probability of being recorded in a given study site, while the conditional Gamma model accounts for differences in the frequency observed among sites considering the number of zeros that are expected according to the error distribution. The

Accepted Article

response variable for the zero-inflated GLM with Gamma distribution was the frequency of mammal records at each station and the explanatory variable was study site. When a mammal species was only recorded in one study site, we applied a GLM with binomial distribution and a logit link function, where the response variable was the presence/absence of the mammal predator species at each station, in order to test whether the difference in probability of occurrence was statistically significant. We also checked for differences in frequency of raptor records between study sites with a GLM with binomial distribution and a logit link function. The response variable was the presence/absence of the raptor predator species per transect over all four visits. We could not subject the data for snakes to statistical analysis because only three captures were made.

Breeding parameters and nest initiation

We tested for differences between study sites in hatching success using a generalized linear mixed model (GLMM) with binomial distribution and logit link function. The response variable was the success or failure of hatching for each egg, and we included nest ID as a random effect to account for the fact that eggs were clustered within nests. As data presented under-dispersion, we analysed the influence of the study sites on clutch size, number of nestlings, and number of fledglings, using linear models with a normally distributed error (McDonald & White 2010). We used a chi-squared test of homogeneity to determine if the nest initiation pattern (i.e. the percentage of nest attempts throughout the breeding season) and nest substrate use differed between study sites.

Nest survival and predation rates

We estimated daily nest survival rate (DSR) and daily nest predation rate with the nest survival model in Program MARK (White & Burnham 1999). We excluded from these analyses 24 nests that were abandoned before egg-laying began. Daily nest predation rate (DSR_p) was estimated considering successful and abandoned nests as not predated and calculating daily nest predation rate as $1-DSR_p$. We calculated nest initiation dates by backdating to the egg-laying stage when nests were found during incubation and successfully hatched. For nests that were found and failed during incubation or nestling stage, we estimated nest age by assuming that the observed period was halfway between the end of laying and hatching or by estimating nestling age, respectively, and backdating accordingly (Dominguez *et al.* 2015). The egg-laying period was considered to last three days, the incubation period 17 days and the nestling period 12 days (Di Giacomo *et al.* 2011). We calculated nest survival and nest predation probabilities as DSR^t and $1-DSR_p^t$, respectively, where t was 32 days, the length of the Strange-tailed Tyrant's nest cycle (Di Giacomo *et al.* 2011).

We used Program MARK to test the effects of several factors that could affect daily nest survival and predation rates. For both nest survival and predation rates analyses, we built candidate models with different combinations of four nest variables: (1) year, (2) a linear trend for the time of breeding (days elapsed since the start of the breeding season, defined as the earliest egg-laying date registered, i.e. 5 September), (3) nest age (days elapsed since the laying of the first egg at day 0) and (4) study site (i.e. INP and REB). We included year and a linear trend for time of breeding to account for interannual and within year changes in weather patterns and predator communities (Dinsmore & Dinsmore 2007). We included nest age to account for the expected increase in predation risk following hatching (Skutch 1949). We used the Akaike information criterion corrected for small sample sizes (AIC_c) to select the best fit models from

the suite of candidate models constructed by combining the variables that had more support than the null-hypothesis model of constant survival, $S(\cdot)$ in MARK notation (Burnham & Anderson 2002). If more than one model had an ΔAIC_c under 2, we selected the one that had the lowest number of parameters and calculated Akaike weights (w_i) to measure the relative support of the models considered (Arnold 2010).

Nest concealment

We used Mann Whitney U -tests to test for differences in nest concealment between successful and predated nests from the overhead and lateral views between study sites and between successful and predated nests.

Unless otherwise specified, we performed all analyses with R 3.6.2 (R Core Team 2019) and used the package *glmmTMB* for zero-inflated GLM with gamma distribution (Brooks *et al.* 2017). We set significance levels at $P < 0.05$ and express results as mean \pm sd.

RESULTS

Nest predator surveys

We did not record top predators in INP, but recorded Pumas three times at three different camera-trap stations in REB. We recorded four mammal nest predator species in INP and five in REB (Table 1). Frequency of mammal records per camera trap per day was significantly higher in INP than in REB; and INP had a higher probability of mammal presence than REB (Table 1). The nest predator with the highest number of records was the Crab-eating Fox *Cerdocyon thous* which was more frequently recorded and had a significantly higher probability of presence in

INP than in REB and (Table 1). The Pampas Fox *Lycalopex gymnocercus* was the second most frequently observed predator and was also significantly more frequently recorded in INP than in REB (Table 1). The frequency of records for both fox species taken together was 10 times higher in INP than in REB, with values of 0.30 and 0.03, respectively. The Maned Wolf *Chrysocyon brachyurus* and Geoffroy's Cat *Leopardus geoffroyi* were only recorded in REB (Table 1). The probability of presence and abundance of Crab-eating Raccoon *Procyon cancrivorus* and Lesser Grison *Galictis cuja* did not differ significantly between study sites (Table 1).

The overall frequency of raptor records was greater in REB than in INP, with two species identified in INP and seven in REB (Table 1). The frequency of records of raptor species did not significantly differ between sites, yet they tended to be less frequently recorded in INP than in REB, except for the Long-winged Harrier *Circus buffoni* and Chimango Caracara *Milvago chimango*, which was only recorded in INP (Table 1).

All snake records occurred in INP, where two Patagonia Green Racers *Philodryas patagoniensis* and one Lichtenstein's Green Racer *Philodryas olfersii* were captured. Average body mass for identified predators can be found in Supporting Information Table S1.

Breeding parameters

The nest initiation pattern of Strange-tailed Tyrants differed between sites ($\chi^2 = 27.7$, $P = 0.001$). It peaked one month earlier in INP (in the second half of September) than in REB (in the second half of October, Fig. 2). Similarly, nest initiation ended in early December in INP, but in late December in REB (Fig. 2).

Breeding parameters did not differ between study sites. Clutch size averaged 2.94 ± 0.41 (range: 2–4, $n = 71$) in INP and 2.88 ± 0.42 (range: 2–4, $n = 120$, $t = 1.10$, $P = 0.27$) in REB.

Hatching success averaged 0.87 ± 0.17 ($n = 39$) in INP and 0.91 ± 0.18 ($n = 59$, $z = -1.54$, $P = 0.13$) in REB. Number of nestlings averaged 2.55 ± 0.61 (range: 1–4, $n = 49$) in INP and 2.66 ± 0.65 (range: 1–4, $n = 73$, $t = -0.91$, $P = 0.37$) in REB. We observed brood reduction in two nests in INP and in eight nests in REB. Fledgling production was 0.52 ± 1.10 chicks per breeding attempt in INP (range: 1–4, $n = 95$) and 0.64 ± 1.16 per breeding attempt in REB (range: 1–4, $n = 151$, $t = 0.39$, $P = 0.39$). Only 21% and 27% of nests where egg-laying began successfully fledged nestlings in INP and REB, respectively. The causes of nest failure were predation and abandonment. Nest predation was responsible for 88% and 75% of nest failure once egg-laying began in INP and REB, respectively, while 12% and 25% were abandoned in INP and REB, respectively. Nest substrate use differed between study sites ($\chi^2 = 180.6$, $P = 0.0005$). The Strange-tailed Tyrant was observed to build its nests on *A. lateralis* ($n = 88$), *P. durifolium* ($n = 1$), *Schizachyrium* spp. ($n = 1$) and on an unidentified species ($n = 3$) in INP and on *A. lateralis* ($n = 27$), *P. intermedium* ($n = 37$) and *I. brasiliensis* ($n = 108$) in REB.

Nest survival and predation rates

When analysing the variables that determined nest survival, we discarded site and year from model building as they performed worse than the null-hypothesis model, and built candidate models with time of breeding and nest age variables. The most parsimonious model included only the variable nest age (Table 2). Daily survival rate decreased with nest age ($\beta = -0.05$; 95% CI: -0.06, -0.03). The average DSR was 0.95 ± 0.004 ($n = 246$) and the cumulative probability of nest survival was 0.18. The DSR were 0.94 ± 0.006 ($n = 95$) and 0.95 ± 0.005 ($n = 151$), with cumulative probabilities of 0.15 and 0.20 in INP and REB, respectively.

When considering the factors that influenced daily nest predation rate, models that included time of breeding, nest age and site performed better than the null-hypothesis model. We discarded year from model building as it performed worse than the constant survival model. The most parsimonious model, and the only one with a $\Delta AIC_c < 2$, included the variables time of breeding, nest age and site (i.e. INP or REB, Table 3). Nest predation rate increased as time of breeding and nest age advanced ($\beta = -0.01$; 95% CI: -0.02, -0.003 and $\beta = -0.05$; 95% CI: -0.07, -0.03, respectively) and was higher in INP than in REB ($\beta = -0.44$; 95% CI: -0.80, -0.08; Fig. 3). The daily nest predation rate was 0.05 ± 0.006 ($n = 95$) and 0.04 ± 0.004 ($n = 151$) with cumulative values of 0.81 and 0.70 in INP and REB, respectively.

Nest predators

Fifteen (21%) of the 71 nests monitored with camera traps in INP were successful, six (9%) were abandoned and 50 (70%) were predated. We were able to identify the nest predator in 27 predation events, a predator identification efficiency of 54%. In addition, a nest containing four nestlings was observed to experience a snake visit, resulting in at least one predated chick and two successfully fledging the nest. In REB, ten (34%) of the 29 monitored nests were successful, four (14%) were abandoned and 15 (52%) were predated. We identified the nest predator on seven occasions, giving a predator identification efficiency of 47%.

The main nest predators in INP were foxes, with 11 predation events by Crab-eating Foxes and three by Pampas Foxes, accounting for 50% of predation events (Table 4). The Patagonia Green Racer predated nine nests, the Chimango Caracara predated three nests and the Crab-eating Raccoon and an unidentified snake predated one nest each (Table 4). We observed a Geoffroy's Cat visiting a nest and, even though no apparent predation took place, we considered

it as a potential nest predator. In addition, we found a predated nest with its original position altered (i.e. fallen) and another nest that was destroyed by the nest predator. Even though these nests were equipped with camera traps we were unable to identify the predator, yet it was probably a mammal. The main nest predator identified in REB was the Maned Wolf, with three predation events (Table 4). The Long-winged Harrier predated two nests and the Roadside Hawk *Rupornis magnirostris* and the Barn Owl *Tyto alba* predated one nest each (Table 4).

Nest concealment

Nest concealment did not differ between study sites, with overhead nest concealment being 0.94 ± 0.12 and 0.93 ± 0.12 ($U = 389$, $P = 0.89$, $n = 58$) and lateral nest concealment of 0.67 ± 0.22 and 0.66 ± 0.18 ($U = 399$, $P = 0.76$, $n = 58$) in INP and REB, respectively. Overhead nest concealment did not differ between successful and predated nests, with values of 0.92 ± 0.16 and 0.94 ± 0.09 , respectively ($U = 341.5$, $P = 0.91$, $n = 58$; Fig. 4a). Lateral nest concealment was greater on successful nests than on predated ones ($U = 237.5$, $P = 0.04$, $n = 58$; Fig. 4b), with values of 0.74 ± 0.19 and 0.63 ± 0.20 , respectively.

DISCUSSION

Nest predator abundances, nest predation, nest concealment and breeding phenology

In accordance with the mesopredator release hypothesis (Soulé *et al.* 1988, Crooks & Soulé 1999), we found the frequency of fox records to be 10 times higher in INP, where top predators were absent, than in REB, where Pumas were detected. We identified foxes as the main nest predators of the Strange-tailed Tyrant, as was found in other study systems (Rogers & Caro

1998, Ritchie & Johnson 2009, Ortega *et al.* 2021). Nest predation rate was high in both study areas but increased with fox abundance.

The mesopredator release hypothesis is not, however, the only possible explanation for the increase in fox abundance observed in INP. The mesopredator release hypothesis is not always supported in manipulative experiments and climatic factors (i.e. bottom-up effects) may be more influential than top-down regulation in some study systems (Castle *et al.* 2021). Differences in food availability or habitat quality could be driving the observed differences in fox abundance. The Crab-eating Fox and the Pampas Fox differ in their habitat preferences (Di Bitetti *et al.* 2022), which may explain their different abundances between sites; and their generalized and opportunistic diets vary between study sites (Di Bitetti *et al.* 2009). These aspects, and lack of replication of study areas, preclude us from concluding that the higher abundance of foxes in INP when compared to REB directly result from the lack of apex predators in the former. However, our results are in accordance with the hypothesis that the extinction of top predators may trigger negative cascading effects on lower trophic levels, including endangered grassland birds (Ritchie & Johnson 2009, Ripple *et al.* 2014, Suraci *et al.* 2016), and further studies should be conducted to test possible bottom-up effects on fox abundance.

Strange-tailed Tyrants had a more synchronized breeding pattern in INP than in REB, with an earlier peak and a shorter breeding season. The shorter breeding season could translate to fewer nesting attempts, thus decreasing the chance of producing a successful brood (Zanette *et al.* 2000). A possible explanation for the differences observed in nest initiation is a shift in arthropod availability, which was previously reported to coincide with the Strange-tailed Tyrant's breeding season (Zermoglio *et al.* 2016). In the present study we did not evaluate if differences in arthropod availability between sites correlated with the differences observed in the

phenology of the breeding season. As breeding synchronization has been hypothesized to result in the dilution of predation pressure (Verhulst & Nilsson 2008), the earlier peak and higher breeding synchronization observed in INP may be an adaptive response to the increased nest predator abundance and nest predation rate. A higher breeding synchronization and earlier breeding of prey species could be an unforeseen consequence of the mesopredator release phenomenon.

Frequency of snake records did not differ between study sites, but nonetheless the Patagonia Green Racer was responsible for a third of nest predation events and was the second main predator in INP. Other studies have also identified snakes as important nest predators (DeGregorio *et al.* 2014, Menezes & Marini 2017, Jeffries *et al.* 2021). We were unable to identify the nest predator in ~45% of nest predation events, and this could have been due to either a delay in camera trap triggering or an inability of camera traps to detect small predators (Ribeiro-Silva *et al.* 2018). Moreover, the camera trap's heat sensor may fail to activate in the presence of cold-blooded snakes. These factors may have caused snake predation events to be under-represented in our study.

Nest concealment is key for avian predation avoidance and Strange-tailed Tyrants had a relatively high overhead nest concealment value of 0.94. This may explain why the higher frequency of raptor records at REB did not translate into a higher predation rate when compared to INP. On the other hand, as also observed in other endangered grassland passerine species, lateral nest concealment was lower on predated nests than on successful ones (Repenning & Fontana 2016, Browne *et al.* 2021). This pattern, in which better concealed nests tended to be more successful, could indicate a strong effect of visually orientated terrestrial predators on nest fate. The study species could also be engaging in antipredator behaviour (i.e. flight-song displays

or coordinated misdirection) aimed at deterring visual predators as reported for other tyrant flycatchers (Pereyra & Morton 2010, Gulson-Castillo *et al.* 2018).

Nest survival, nest predation and breeding parameters

Nest predation rate was higher in INP than in REB and overall breeding success of Strange-tailed Tyrants was low. Increased predation is more threatening when population sizes are small, as is the case with endangered species, potentially accentuating inbreeding and decreasing genetic variation (Frankham 1995). Nonetheless, natural selection may favour reduced clutch sizes and increased breeding attempts to maximize breeding success when predation rates are high (Roper *et al.* 2010). Strange-tailed Tyrant females have been reported to achieve an average of two nest attempts per breeding season (range, 1-4) because of nest failure but double-brooding (i.e. two successful attempts per breeding season) was only rarely recorded (Di Giacomo *et al.* 2011). In addition, 17 days were reported to elapse between nesting attempts (Di Giacomo *et al.* 2011). Given that the breeding season was observed to end earlier in INP, females may have fewer re-nesting opportunities here than in REB. Future studies should consider multiple breeding attempts, clutch replacement and genetic variation to evaluate more accurately the impact of the increased nest predation rate observed in INP on the Strange-tailed Tyrant. Also, as overall breeding success was low, the population viability of this endangered species should be assessed considering other life history traits.

The Strange-tailed Tyrant's nest survival and nest predation rate were both modulated by nest age, while nest predation rate also varied between study sites and was dependent on time of breeding. The finding that nest predation rates differed between protected areas while nest survival did not could be due to the higher nest abandonment rate observed in REB. A potential

Accepted Article

cause for nest abandonment is adult predation by raptors. The higher raptor abundance detected in REB could thus explain the higher nest abandonment rate detected in this protected area, where raptor predation events on adult Strange-tailed Tyrants individuals were registered (Di Giacomo & Krapovickas 2005). Nest abandonment could also be caused by nest flooding, which was previously reported to be the main cause of abandonment of Strange-tailed Tyrant nests in REB but was not observed in INP (Di Giacomo *et al.* 2011). Both nest survival and predation rates were influenced by nest age, which is in accordance with the expected increase in predation rate as nest activity increases (Skutch 1949). The observed increase in nest predation rate as the breeding season advanced could be due to a predator functional response, mediated either by the development of a search image or by prey switching (i.e. consumption rate varies according to prey availability), or to a synchronization in prey-predator breeding timing (Roos 2002, Verhulst & Nilsson 2008, Randa *et al.* 2009). Future studies should assess variations in predator abundance and behaviour throughout the breeding season.

Nest substrate use differed between study sites. Female Strange-tailed Tyrants were not observed to build their nests on *Paspalum* stands in INP, while in REB they did. Interspecific competition for nesting sites between the study species and the Black-and-white Monjita *Xolmis dominicanus* could be taking place in INP. The Black-and-white Monjita uses *Paspalum* as a nest substrate but does not occur in REB. This larger tyrant could be limiting the breeding territory available for the Strange-tailed Tyrant in INP (Sætre *et al.* 1999, Carrete *et al.* 2006). Nest substrate choice and interspecific competition deserve further study to better understand the driving factors of nest substrate use.

Some Strange-tailed Tyrant breeding parameters were similar between sites, with no differences found in clutch size, hatching success and fledgling production. These values were

similar to those previously reported for the study species (Di Giacomo *et al.* 2011). The lack of differences in these breeding parameters could imply that they are not responsive to increased nest predation risk or that trade-offs in adaptive responses are involved. Future studies should consider variations in egg size and clutch mass as possible responses to increased nest predation risk (Fontaine & Martin 2006).

Conclusions

The majority of the Strange-tailed Tyrant's distribution range is on private lands dedicated mainly to afforestation or livestock production. Previous studies have indicated that high levels of grazing would not sustain populations of endangered grassland species, such as our study species (Di Giacomo *et al.* 2010). Our findings are also discouraging, as we found the breeding success of an endangered species in protected areas to be relatively low. A population viability model of the Strange-tailed Tyrant should be conducted to better orientate conservation efforts and guarantee the persistence of one of the last populations of this threatened species.

If the differences in breeding parameters reported here are indeed the result of mesopredator release, the recent reintroduction of Jaguars in the Iberá Wetlands provides a promising scenario for endangered birds breeding in the protected area (Donadio *et al.* 2022). The restoration of top predators has been found to reduce mesopredator abundances (Jiménez *et al.* 2019). Indeed, two fox predation events by the Jaguars released in INP in January 2021 have been registered (Q. Gómez pers. comm.). Mesocarnivore control has been reported to increase nest success and bird populations (Palmer *et al.* 2019). In addition, our results illustrate the negative effect the release of native predators, often considered to be less harmful than alien predators, may have on native prey species, such as endangered grassland birds (Salo *et al.*

2007). Likewise, we expect nest predation rates to decrease as mesopredator populations, particularly of foxes, stabilize at lower levels under the renewed presence of a top predator, 50 years after its extinction in the Iberá Wetlands.

ACKNOWLEDGEMENTS

We thank the Administración de Parques Nacionales, the Dirección de Parques y Reservas de Corrientes, and the Dirección de Recursos Naturales for granting us permission to work in Iberá National Park (permit number: IF-2018-53280705-APN-DRNEA#APNAC) and Alparamis S.A. and Aves Argentinas for allowing us to work in Reserva El Bagual. We also thank A.C. Giese for her help in data analysis, M. Álvarez Correa, D.G. Barcos, F. Bres, C. Bruzzese, B. Cortés, H.H. Correa, A.B. Fariña, N.V. Got, A. Moreira, G. Reyes Benz, F. Sánchez Gavier, and F. N. Zarza for their assistance in the field and the Associate Editor, Alexandre Millon, and two anonymous reviewers for providing many helpful comments to improve the manuscript.

Funding Statement: This study was supported by grants from the Neotropical Grassland Conservancy, the Neotropical Bird Club, the Association of Field Ornithologists, the American Society of Mammalogists, Agencia Nacional de Promoción Científica y Tecnológica [PICT 2014-3397, PICT 2018-3407], and CONICET [PUE 229 20180100001 CO]. The funding sources had no involvement in study design, data collection, analysis, and interpretation, writing of the manuscript, nor in the decision to submit the article for publication.

Author Contributions: M.B.: Formal analysis, Methodology, Investigation, Data curation, Funding acquisition, Writing – Original Draft, Visualization. C.P.: Methodology, Data curation, Investigation, Funding acquisition, Writing – Review & Editing. A.G.D.G: Data curation, Investigation, Resources. M.S.D.B.: Methodology, Conceptualization, Resources, Writing – Review & Editing. A.S.D.G.:

Methodology, Conceptualization, Supervision, Writing – Original Draft, Project administration, Funding acquisition.

Data availability statement: All scripts and files needed to reproduce our analyses will be archived in Mendeley Data upon acceptance.

REFERENCES

- Arnold, T.W.** 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manag.* 74(6): 1175–1178.
- Azpiroz, A.B., Isacch, J.P., Dias, R.A., Di Giacomo, A.S., Fontana, C.S. & Palarea, C.M.** 2012. Ecology and conservation of grassland birds in southeastern South America: a review. *J. Field Orn.* 83: 217–246.
- BirdLife International.** 2016. *Alectrurus risora*. *The IUCN Red List of Threatened Species* 2016: e.T22700303A93768087. <https://www.iucnredlist.org/species/22700303/93768087>
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M. & Bolker, B.M.** 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9(2): 378–400.
- Browne, M., Turbek, S.P., Pasian, C. & Di Giacomo, A.S.** 2021. Low reproductive success of the endangered Iberá Seedeater in its only known breeding site, the Iberá Wetlands, Argentina. *Ornithol. Appl.* 123: duab008.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer-Verlag.

- Carnevali, R.** 1994. *Fitogeografía de la Provincia de Corrientes*. Corrientes: Gobierno de la Provincia de Corrientes-INTA.
- Carrete, M., Sánchez-Zapata, J.A., Tella, J.L., Gil-Sánchez, J.M. & Moleón, M.** 2006. Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. *Oikos* 112: 680–690.
- Castle, G., Smith, D., Allen, L.R. & Allen, B.L.** 2021. Terrestrial mesopredators did not increase after top-predator removal in a large-scale experimental test of mesopredator release theory. *Sci. Rep.* 11(1): 1–18.
- Crooks, K.R. & Soulé, M.E.** 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563–566.
- Davis, S.K.** 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor* 107: 605–616.
- DeGregorio, B.A., Chiavacci, S.J., Weatherhead, P.J., Willson, J.D., Benson, T.J. & Sperry, J.H.** 2014. Snake predation on North American bird nests: culprits, patterns and future directions. *J. Avian Biol.* 45: 325–333.
- Di Bitetti, M.S., De Angelo, C.D., Quiroga, V., Altrichter, M., Paviolo, A., Cuyckens, E. & Perovic, P.** 2016. Estado de conservación del jaguar en la Argentina. In Medellín, R.A., Antonio J.T. & Heliot Z., Cuauhtémoc Chávez & Gerardo Ceballos (eds) *El jaguar en el siglo XXI. La perspectiva continental*. Mexico, Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Instituto de Ecología.
- Di Bitetti, M.S., Di Blanco, Y.E., Pereira, J.A., Paviolo, A. & Jiménez Pérez, I.** 2009. Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cerdocyon thous*) and pampas foxes (*Lycalopex gymnocercus*). *J. Mammal.* 90: 479–490.

- Di Bitetti, M.S., Iezzi, M.E., Cruz, P., Cirignoli, S., Varela, D. & De Angelo, C.** 2022. Enemies or good neighbors? No indication of spatial or temporal avoidance between two sympatric South American canids. *J. Zool.* 317(3): 170–184.
- Di Giacomo A.G. & Krapovickas, S.F.** 2005. *Historia Natural y Paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina. Inventario de la Fauna de Vertebrados y de la Flora Vasculare de un Área Protegida del Chaco Húmedo.* Buenos Aires: Aves Argentinas/Asociación Ornitológica del Plata.
- Di Giacomo, A.S., Vickery, P.D., Casanas, H., Spitznagel, O.A., Ostrosky, C., Krapovickas, S. & Bosso, A.J.** 2010. Landscape associations of globally threatened grassland birds in the Aguapey river Important Bird Area, Corrientes, Argentina. *Bird Conserv. Int.* 20(1): 62–73.
- Di Giacomo, A.S., Di Giacomo, A.G. & Reboreda, J.C.** 2011. Male and female reproductive success in a threatened polygynous species: the Strange-tailed Tyrant, *Alectrurus risora*. *Condor* 113: 619–628.
- Di Giacomo, A.S. & Di Giacomo, A.G.** 2004. Extinción, historia natural y conservación de las poblaciones del Yetapá de Collar (*Alectrurus risora*) en la Argentina. *Ornitol. Neotrop.* 15: 145–157.
- Dillon, K.G. & Conway, C.J.** 2018. Nest predation risk explains variation in avian clutch size. *Behav. Ecol.* 29: 301–311.
- Dinsmore, S.J. & Dinsmore, J.J.** 2007. Modeling avian nest survival in program MARK. *Stud. Avian Biol.* 34: 73.
- Dominguez, M., Reboreda, J.C. & Mahler, B.** 2015. Impact of Shiny Cowbird and botfly parasitism on the reproductive success of the globally endangered Yellow Cardinal *Gubernatrix cristata*. *Bird Conserv. Int.* 25(3): 294–305.

- Donadio, E., Di Martino, S. & Heinonen, S.** 2022. Rewilding Argentina: lessons for the 2030 biodiversity targets. *Nature* 603: 225–227
- Fontaine, J.J. & Martin, T.E.** 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* 9: 428–434.
- Frankham, R.** 1995. Effective population size/adult population size ratios in wildlife: a review. *Genet. Res. Int.* 66: 95–107.
- Graham, K., Beckerman, A.P. & Thirgood, S.** 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biol. Conserv.* 122:159–171.
- Gulson-Castillo, E.R., Greeney, H.F. & Freeman, B.G.** 2018. Coordinated misdirection: a probable anti-nest predation behavior widespread in Neotropical birds. *Wilson J. Ornithol.* 130: 583–590.
- Hoekstra, J.M., Boucher, T.M., Ricketts, T.H. & Roberts, C.** 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.* 8: 23–29.
- Jefferies, M.M., Coria, P.S.G. & Llambías, P.E.** 2021. Nest predator identity and nest predation rates of three songbirds in the central Andes of south temperate Argentina. *Wilson J. Ornithol.* 133: 117–124.
- Jiménez, J., Nuñez-Arjona, J.C., Mougeot, F., Ferreras, P., González, L.M., García-Domínguez, F., Muñoz-Igualada, J., Palacios, M.J., Pla, S., Ruega, C., Villaespesa, F., Nájera, F., Palomares, F. & López-Bao, J.V.** 2019. Restoring apex predators can reduce mesopredator abundances. *Biol. Conserv.* 238:108234.
- Leynaud, G.C. & Bucher, E.H.** 2005. Restoration of degraded Chaco woodlands: effects on reptile assemblages. *For. Ecol. Manage.* 213: 384–390.

- McDonald, T.L. & White, G.C.** 2010. A comparison of regression models for small counts. *J. Wildl. Manag.* 74(3): 514–521.
- Martin, T.E.** 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65: 101–127.
- Martin, T.E. & Geupel, G.R.** 1993. Nest-monitoring plots: Methods for locating nests and monitoring success. *J Field Ornithol.* 64: 507–519.
- Martin, T.E. & Roper, J.J.** 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90: 51–57.
- Menezes, J.C. & Marini, M.Â.** 2017. Predators of bird nests in the Neotropics: a review. *J. Field Orn.* 88: 99–114.
- Misenhelter, M.D. & Rotenberry, J.T.** 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81: 2892–2901.
- O’Connell, A.F., Nichols, J.D. & Karanth, K.U. (eds)** 2011. *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, Japan.
- Ortega, S., Rodríguez, C., Mendoza-Hernández, B. & Drummond, H.** 2021. How removal of cats and rats from an island allowed a native predator to threaten a native bird. *Biol. Invasions* 1–13.
- Oyarzabal, M., Clavijo, J.R., Oakley, L.J., Biganzoli, F., Tognetti, P.M., Barberis, I.M., Maturo, H.M., Aragón, R., Campanello, P.I., Prado, D., Oesterheld, M. & León, R.J.C.** 2018. Unidades de vegetación de la Argentina. *Ecol. Austral* 28: 040–063.
- Palmer, W.E., Carroll, J.P., Sisson, D.C., Wellendorf, S.D., Terhune, T.M., Ellis-Felege, S.N. & Martin, J.A.** 2019. Reduction in meso-mammal nest predators improves northern bobwhite demographics. *J. Wildl. Manage.* 83: 646–656.

- Pereyra, M.E. & Morton, M.L.** 2010. Flight songs of Dusky Flycatchers: a response to bird-hunting raptors? *J. Field Orn.* 81: 42–48.
- Quiroga, V.A., Boaglio, G.I., Noss, A.J. & Di Bitetti, M.S.** 2014. Critical population status of the jaguar in the Argentine Chaco: Camera trap surveys suggest recent collapse and imminent regional extinction. *Oryx* 48(1): 141–148.
- Quiroga, V.A., Noss, A.J., Paviolo, A., Boaglio, G.I. & Di Bitetti, M.S.** 2016. Puma density, habitat use and conflict with humans in the Argentine Chaco. *J. Nat. Conserv.* 31: 9–15.
- R Core Team.** 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ralph, C.J., Geupel, G.R., Pyle, P., Martin, T.E. & DeSante, D.F.** 1993. *Handbook of Field Methods for Monitoring Landbirds*. Albany: Pacific Southwest Research Station.
- Randa, L.A., Cooper, D.M., Meserve, P.L. & Yunker, J.A.** 2009. Prey switching of sympatric canids in response to variable prey abundance. *J. Mammal.* 90: 594–603.
- Rees J.D., Kingsford, R.T. & Letnic, M.** 2019. Changes in desert avifauna associated with the functional extinction of a terrestrial top predator. *Ecography* 42: 67–76.
- Repenning, M. & Fontana, C.S.** 2016. Breeding biology of the Tropeiro Seedeater (*Sporophila beltoni*). *Auk* 133: 484–496.
- Ribeiro-Silva, L., Perrella, D.F., Biagolini-Jr, C.H., Zima, P.V., Piratelli, A.J., Schlindwein, M.N., Galetti Junior, P.M. & Francisco, M.R.** 2018. Testing camera traps as a potential tool for detecting nest predation of birds in a tropical rainforest environment. *Zoologia (Curitiba)* 35: e14678.
- Ricklefs, R.E.** 1969. *An Analysis of Nesting Mortality in Birds*. Washington: Smithsonian contributions to zoology.

- Ritchie, E.G. & Johnson, C.N.** 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12: 982–998.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J.** 2014. Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484.
- Rogers, C.M. & Caro, M.J.** 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. *Oecologia* 116(1): 227–233.
- Roos, S.** 2002. Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* 133: 608–615.
- Roos, S., Smart, J., Gibbons, D.W. & Wilson, J.D.** 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. *Biol.* 93(4): 1915–1937.
- Roper, J.J., Sullivan, K.A. & Ricklefs, R.E.** 2010. Avoid nest predation when predation rates are low, and other lessons: testing the tropical–temperate nest predation paradigm. *Oikos* 119(4): 719–729.
- Saggiomo, L., Bar, V. & Esattore, B.** 2021. The fox who cried wolf: A keywords and literature trend analysis on the phenomenon of mesopredator release. *Ecol. Complex.* 48: 100963.
- Salo, P., Korpimäki, E., Banks, P.B., Nordström, M. & Dickman, C.R.** 2007. Alien predators are more dangerous than native predators to prey populations. *Proc. R. Soc. Lond. B* 274: 1237–1243.
- Sætre, G.P., Post, E. & Král, M.** 1999. Can environmental fluctuation prevent competitive exclusion in sympatric flycatchers? *Proc. R. Soc. Lond. B* 266: 1247–1251.

- Schmidt, K.A.** (2003). Nest predation and population declines in Illinois songbirds: a case for mesopredator effects. *Conserv. Biol.* 17(4): 1141–1150.
- Schmidt, K.A. & Whelan, C.J.** 1999. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conserv. Biol.* 13: 1502–1506.
- Skutch, A.F.** 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430–455.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M. & Hill, S.** 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2(1): 75–92.
- Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y.** 2016. Fear of large carnivores causes a trophic cascade. *Nat. Commun.* 7: 1–7.
- Verhulst, S. & Nilsson, J.Å.** 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 363: 399–410.
- Viglizzo, E.F., Frank, F.C., Carreño, L.V., Jobbagy, E.G., Pereyra, H., Clatt, J., Pincen, D. & Ricard, M.F.** 2011. Ecological and environmental footprint of 50 years of agricultural expansion in Argentina. *Glob. Chang. Biol.* 17: 959–973.
- Watson, J.E., Jones, K.R., Fuller, R.A., Marco, M.D., Segan, D.B., Butchart, S.H., Allan, J.R., McDonald-Madden, E. & Venter, O.** 2016. Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. *Conserv. Lett.* 9: 413–421.
- White, G.C. & Burnham, K.P.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120–138.

Zanette, L., Doyle, P. & Trémont, S.M. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81: 1654–1666.

Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334: 1398–1401.

Zermoglio, P.F., Di Giacomo, A.S., Di Giacomo, A.G. & Castelo, M.K. 2016. Arthropod prey availability and breeding of the threatened Strange-tailed Tyrant (*Alectrurus risora*). *Ornitol. Neotrop.* 27: 259–266.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Average body mass of identified predators.

Figure S1. Illustrative photos of nests and disk placement for concealment analysis.

Table 1. Potential nest predator frequency of records in Reserva El Bagual (REB; top predators present) and Iberá National Park (INP; top predators absent), Argentina, and summary statistics. Mammal frequency of records is expressed as the number of records per station divided by the number of days the station was active and raptor frequency of records as the number of records per transect, total number of records are expressed in parenthesis. In the models, the response variables are; mammal frequency of records expressed as the number of records per station divided by the number of days the station was active for mammals present in both sites and as presence/absence per camera station for mammal species present in one study site and presence/absence per transect for raptors. Models applied: gamma zero-inflated GLM for Crab-eating Fox, Lesser Grison, Crab-eating Raccoon and overall mammal frequency of records. $z(a)$ = z-value of conditional Gamma model, $P(a)$ = p-value of conditional Gamma model, $z(b)$ = z-value of zero-inflated model, $P(b)$ = p-value of zero-inflated model. For the remaining mammal species which occurred in only one study area and for raptors, a binomial GLM test (z = z-value; P = p-value) tests whether the difference in probability of occurrence between study areas is statistically significant. Highest frequencies are highlighted in bold when significant.

Species	Common name	REB	INP	$z(a)$	$P(a)$	$z(b)$	$P(b)$
Mammals							
<i>Cerdocyon thous</i>	Crab-eating Fox	2.0 (47)	13.6 (354)	-2.08	0.04	-3.63	2.79e-4
<i>Chrysocyon brachyurus</i>	Maned Wolf	0.7 (17)	0 (0)	-1.56	0.12		
<i>Lycalopex gymnocercus</i>	Pampas Fox	0 (0)	5.7 (147)	3.11	1.89e-3		
<i>Leopardus geoffroyi</i>	Geoffroy's Cat	0.5 (11)	0 (0)	-0.71	0.48		
<i>Galictis cuja</i>	Lesser Grison	0.1 (3)	0.2 (5)	-1.47	0.14	-0.29	0.77

<i>Procyon cancrivorus</i>	Crab-eating Raccoon	1.1 (27)	0.3 (8)	1.45	0.15	1.42	0.16
Total		4.4 (105)	19.8 (514)	-4.11	3.95e-5	-1.99	0.04

Raptors

<i>Rupornis magnirostris</i>	Roadside Hawk	0.5 (1)	0 (0)	-0.003	0.99		
<i>Circus buffoni</i>	Long-winged Harrier	2.0 (4)	0.5 (3)	0.003	0.99		
<i>Buteo albicaudatus</i>	White-tailed Hawk	2.5 (5)	0 (0)	-0.003	0.99		
<i>Heterospizias meridionalis</i>	Savanna Hawk	1.0 (2)	0 (0)	-0.003	0.99		
<i>Milvago chimango</i>	Chimango Caracara	0 (0)	2.3 (14)	0.003	0.99		
<i>Milvago chimachima</i>	Yellow-headed Caracara	1.0 (2)	0 (0)	-0.003	0.99		
<i>Falco femoralis</i>	Aplomado Falcon	1.0 (2)	0 (0)	-0.003	0.99		
<i>Falco sparverius</i>	American Kestrel	4.0 (8)	0 (0)	-0.003	0.99		
Total		12.0 (24)	2.8 (17)	-2.14	0.03		

Table 2. Support for models predicting daily survival rate of Strange-tailed Tyrant nests throughout four breeding seasons from 2015 to 2018 in Iberá National Park and Reserva El Bagual, Argentina ($n = 246$). T = linear term for time of breeding; AIC_c = Akaike's information criteria corrected for small sample size; ΔAIC_c = difference in AIC_c relative to the best model; k = number of parameters; w_i = model weight.

Model	ΔAIC_c	k	w_i
$S(T + \text{Nest age})$	0.0 ^a	3	0.67
$S(\text{Nest age})$	1.4	2	0.33
$S(T)$	19.2	2	0.00
$S(\cdot)$	25.5	1	0.00
$S(\text{Site})$	26.1	2	0.00
$S(\text{Year})$	29.5	4	0.00

^a $AIC_c = 1063.7$

Table 3. Support for models predicting daily nest predation rate of Strange-tailed Tyrant nests throughout four breeding seasons from 2015 to 2018 in Iberá National Park and Reserva El Bagual, Argentina ($n = 246$). T = linear term for time of breeding; AIC_c = Akaike's information criteria corrected for small sample size; ΔAIC_c = difference in AIC_c relative to the best model; k = number of parameters; w_i = model weight.

Model	ΔAIC_c	k	w_i
S (Nest age + T + Site)	0.0 ^a	4	0.78
S (Nest age + T)	3.6	3	0.13
S (Nest age + Site)	5.3	3	0.05
S (Nest age)	5.8	2	0.04
S (T + Site)	24.2	3	0.00
S (T)	31.9	2	0.00
S (Site)	38.8	2	0.00
S (.)	40.7	1	0.00
S (Year)	43.3	4	0.00

^a $AIC_c = 891.2$

Table 4. Percentage of nest predation events in Reserva El Bagual (REB; 7 predation events), where top predators are present, and Iberá National Park (INP, 28 predation events), where they are not.

Species	Common name	REB	INP
Mammals			
<i>Cerdocyon thous</i>	Crab-eating Fox	0	11
<i>Chrysocyon brachyurus</i>	Maned Wolf	3	0
<i>Lycalopex gymnocercus</i>	Pampas Fox	0	3
<i>Leopardus geoffroyi</i>	Geoffroy's Cat	0	0
<i>Galictis cuja</i>	Lesser Grison	0	0
<i>Procyon cancrivorus</i>	Crab-eating Raccoon	0	1
Total		3	15
Raptors			
<i>Rupornis magnirostris</i>	Roadside Hawk	1	0
<i>Circus buffoni</i>	Long-winged Harrier	2	0
<i>Buteo albicaudatus</i>	White-tailed Hawk	0	0
<i>Heterospizias meridionalis</i>	Savanna Hawk	0	0
<i>Milvago chimango</i>	Chimango Caracara	0	3
<i>Milvago chimachima</i>	Yellow-headed Caracara	0	0
<i>Falco femoralis</i>	Aplomado Falcon	0	0
<i>Falco sparverius</i>	American Kestrel	0	0
<i>Tyto alba</i>	Barn Owl	1	0
Total		4	3

Snakes

<i>Philodryas patagoniensis</i>	Patagonia Green Racer	0	9
<i>Philodryas olfersii</i>	Lichtenstein's Green Racer	0	0
	Unidentified snake	0	1
Total		0	10

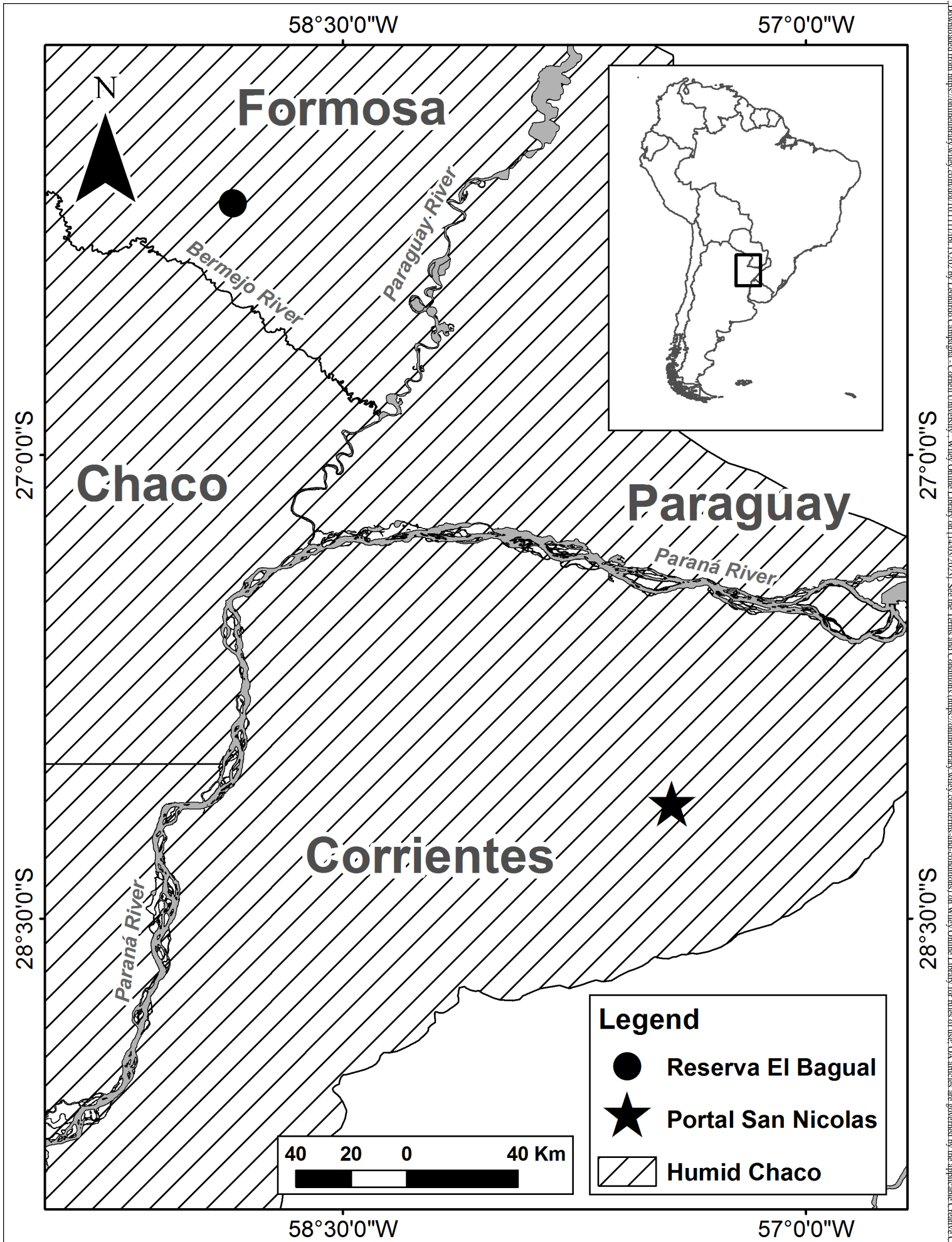
Figure Legends

Figure 1. Location of the study sites, Portal San Nicolás (Iberá National Park - INP), located in the province of Corrientes, and Reserva El Bagual (REB), located in the province of Formosa, north-eastern Argentina.

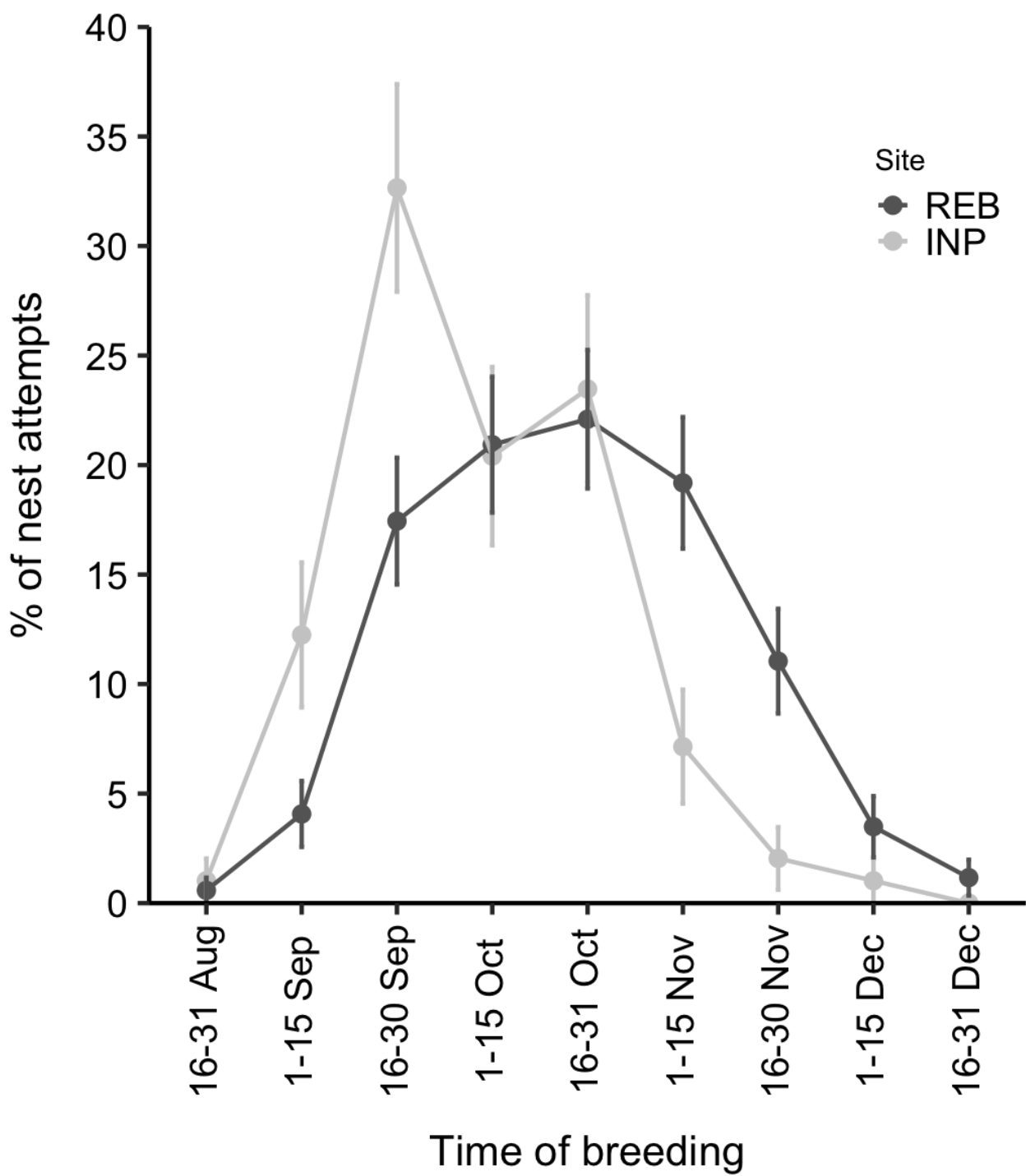
Figure 2. Percentage of nest attempts by female Strange-tailed Tyrants during the breeding seasons of 2015–2018 in Reserva El Bagual (REB) and Iberá National Park (INP, $n = 270$ nests), Argentina. Error bars are standard errors.

Figure 3. Variation in daily nest predation rate of Strange-tailed Tyrant nests during (a) incubation and (b) nestling stage in the presence/absence of top predators in Reserva El Bagual (REB) and Iberá National Park (INP), respectively, throughout the breeding seasons of 2015–2018 ($n = 246$ nests), Argentina. Solid lines are mean nest predation rate values; dashed lines are standard error values.

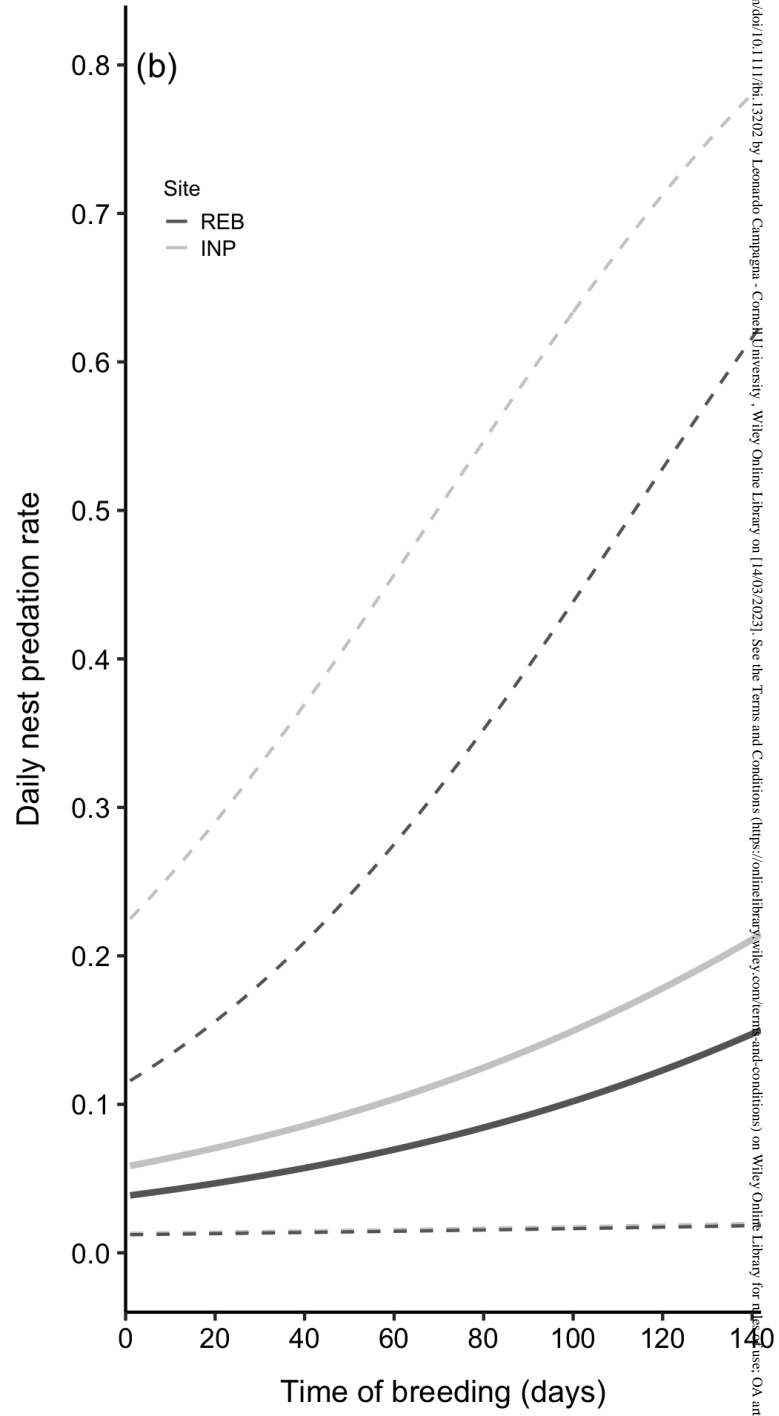
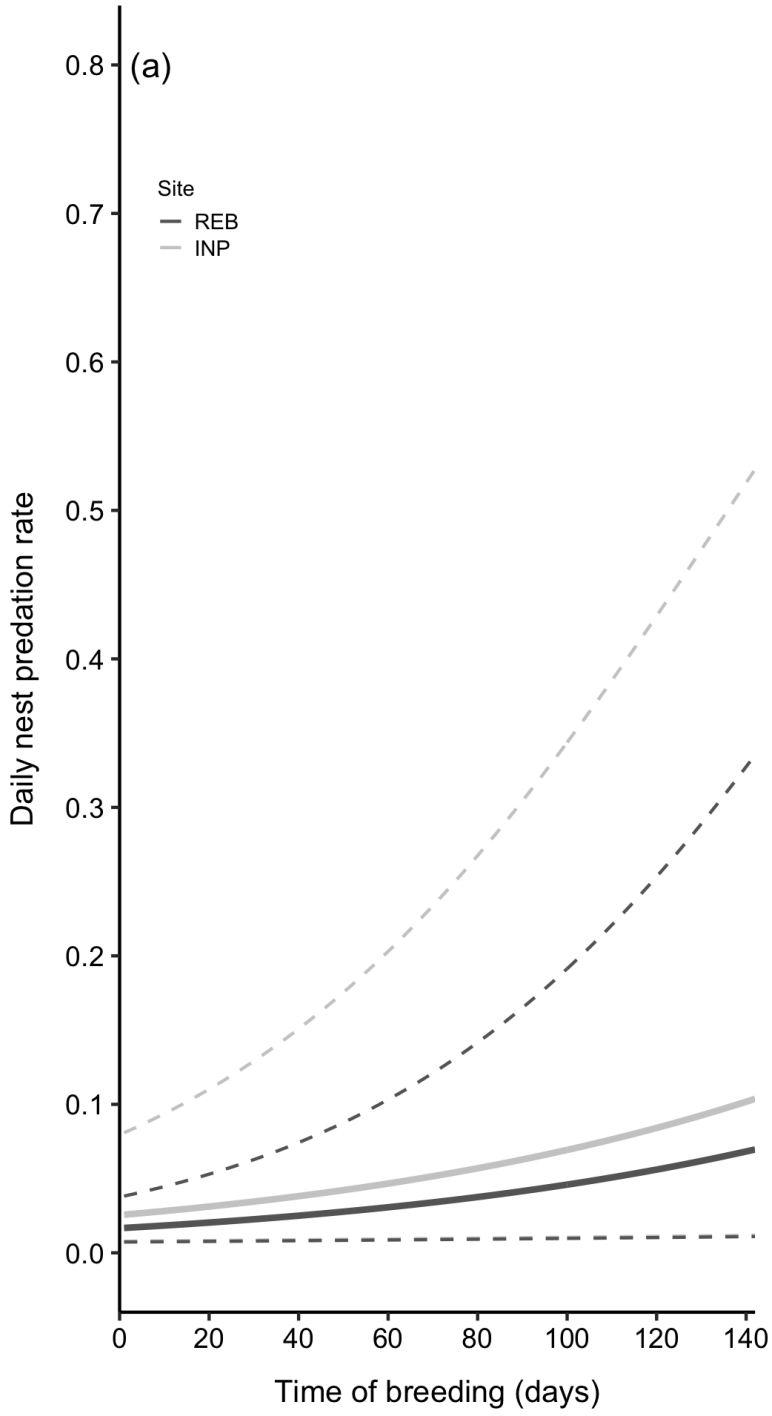
Figure 4. Average (a) overhead and (b) lateral nest concealment of successful and predated Strange-tailed Tyrant nests ($n = 58$) found during the 2017 and 2018 breeding seasons in Reserva El Bagual (REB) and Iberá National Park (INP), Argentina. Error bars are standard errors.



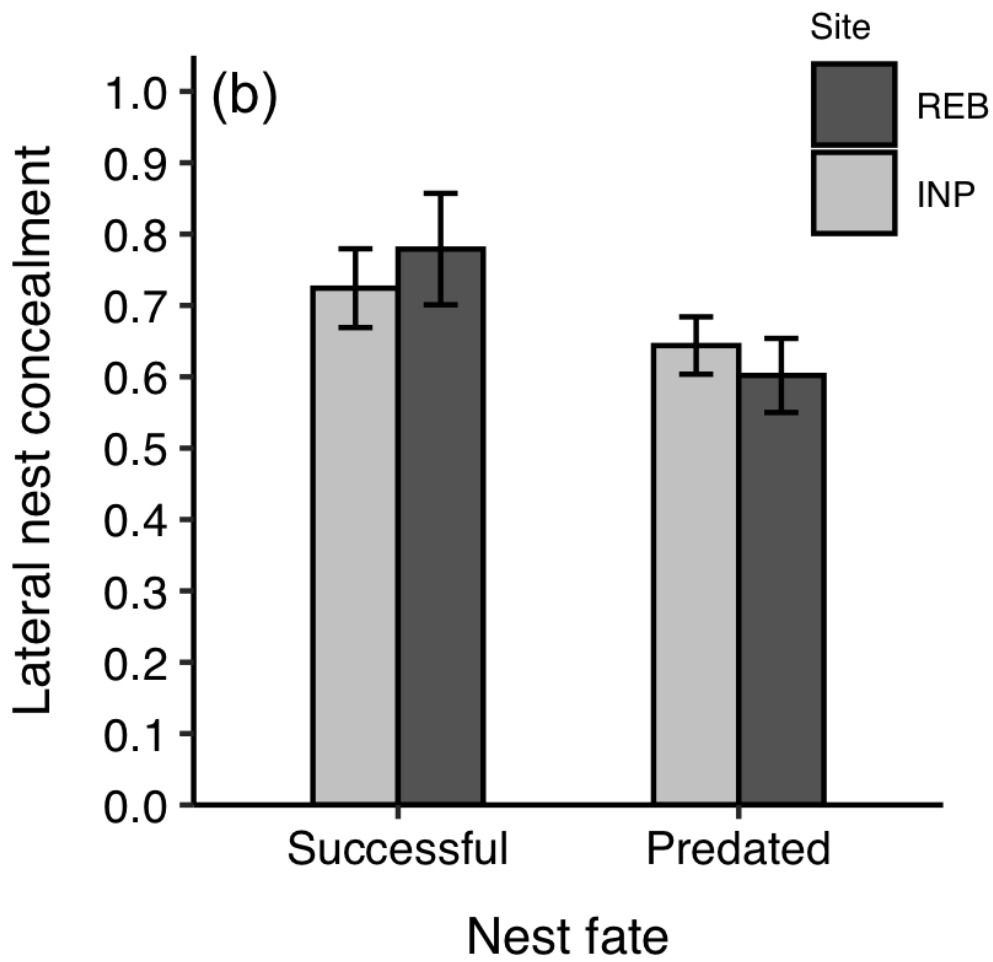
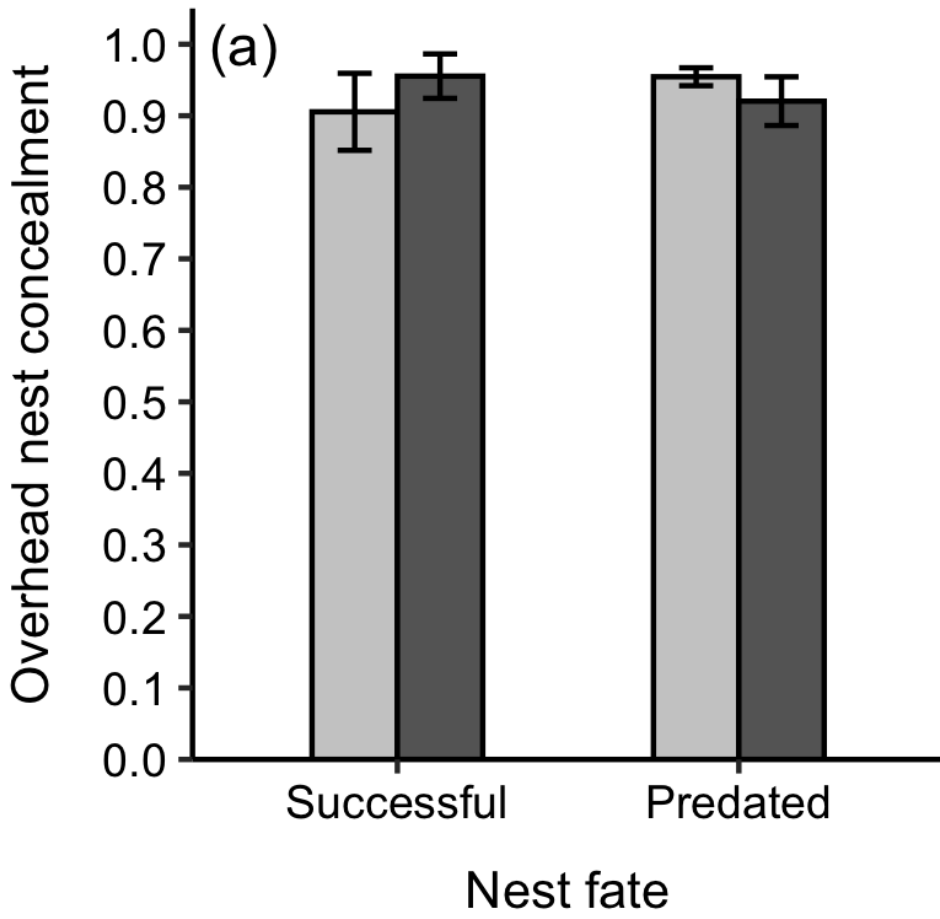
IBI_13202_Figure 1.tif



IBI_13202_Figure 2.tif



IBI_13202_Figure 3.tiff



IBI_13202_Figure 4.tif