Nest-site selection and breeding success of passerines in the world's southernmost forest

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Background. Birds can maximize their reproductive success through careful selection of nest-sites. The 'total-foliage' hypothesis predicts that nests concealed in vegetation should have higher survival. We propose an additional hypothesis, the 'predator proximity' hypothesis, which states that nests placed further from predators would have higher survival. We examined these hypotheses at the world's southernmost forests of Navarino Island, in the Cape Horn Biosphere reserve, Chile (55°S). This island has been free of ground predators until recently, and forest passerines have been subject to depredation only by diurnal and nocturnal raptors.

Methods. During three breeding seasons (2014 – 2017), we monitored 104 nests for the five most abundant open-cup forest-dwelling passerines (*Elaenia albiceps*, *Zonotrichia capensis*, *Phrygilus patagonicus*, *Turdus falcklandii*, and *Anairetes parulus*). We identified nest predators using camera traps and assessed whether habitat characteristics affected nest-site selection and survival.

Results. Nest predation was the main cause of nest failure (71% of failed nests). *Milvago chimango* was the most common predator, depredating 13 (87%) of the 15 nests where we could identify a predator. Whereas the recently introduced mammal, *Neovison vison*, the only ground predator, depredated one nest (7%). Species selected nest-sites with more understory cover and taller understory which, according to the total-foliage hypothesis, would provide more concealment against both avian and mammal predators. However, these variables negatively influenced nest survival. The apparent disconnect between selecting nest-sites to avoid predation and the actual risk of predation could be due to recent changes in the predator assemblage driven by an increased abundance of native *M. chimango* associated with urban development, and/or the introduction of exotic mammalian ground predators to this island. These predator assemblage changes could have resulted in an ecological trap. Further research will be needed to assess hypotheses that could explain this mismatch between nest-site selection and nest survival.

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23

24 **Abstract**

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26 sites. The 'total-foliage' hypothesis predicts that nests concealed in vegetation should have

27 higher survival. We propose an additional hypothesis, the 'predator proximity' hypothesis, which

28 states that nests placed further from predators would have higher survival. We examined these

29 hypotheses at the world's southernmost forests of Navarino Island, in the Cape Horn Biosphere

30 reserve, Chile (55°S). This island has been free of ground predators until recently, and forest

31 passerines have been subject to depredation only by diurnal and nocturnal raptors.

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37 **Results.** Nest predation was the main cause of nest failure (71% of failed nests). *Milvago*

38 *chimango* was the most common predator, depredating 13 (87%) of the 15 nests where we could

39 identify a predator. Whereas the recently introduced mammal, *Neovison vison*, the only ground

40 predator, depredated one nest (7%). Species selected nest-sites with more understory cover and

41 taller understory which, according to the total-foliage hypothesis, would provide more

42 concealment against both avian and mammal predators. However, these variables negatively

43 influenced nest survival. The apparent disconnect between selecting nest-sites to avoid predation

44 and the actual risk of predation could be due to recent changes in the predator assemblage driven

45 by an increased abundance of native *M. chimango* associated with urban development, and/or the

46 introduction of exotic mammalian ground predators to this island. These predator assemblage

47 changes could have resulted in an ecological trap. Further research will be needed to assess

48 hypotheses that could explain this mismatch between nest-site selection and nest survival.

49

50 **Introduction**

51 Where do birds place their nests? This question has intrigued ornithologists since the early days

52 of the discipline (Birkhead et al. 2014, Lovette and Fitzpatrick 2016). For open-cup nesters, early

53 studies pointed to food availability as the most important factor for nest site selection, but

54 predation has been increasingly considered as another major factor (Martin 1987, 1993; Reidy

55 and Thompson 2018). Predation can directly affect survival of eggs, juveniles, and adults, and

56 has been identified as the main cause of nest failure in passerines (Nice 1957, Ricklefs 1969,

57 Liebezeit and George 2002, Bellamy et al. 2018, Reidy and Thompson 2018). According to these

58 studies, we predict that birds will select those habitat characteristics that reduce predation risk

59 and thus increase the probabilities of nest survival (Jaenike and Holt 1991, Fontaine and Martin

60 2006).

61   Several hypotheses have been proposed to explain the mechanisms by which nest

62 placement reduces predation. One of these, the 'total-foliage' hypothesis, predicts that nests

63 located in sites with more surrounding foliage would have higher concealment, as well as more

64 interference with the transmission of odors and sounds that could be detected by a predator.

65 Thus, a larger amount of foliage reduces predation risk (Martin and Roper 1988, Martin 1993).

66 In the present study we introduce another, but not mutually exclusive hypothesis, which we call

67 the 'predator proximity' hypothesis. This hypothesis assesses types of predators according to

68 their mode of attack, particularly aerial versus terrestrial. This hypothesis assumes that passerine

69 birds select nest sites that avoid discovery and attack by the major type of predators in their

70   ecosystem, and it predicts that: (i) when predation is dominated by aerial predators, birds will

71   place nests near the ground and (ii), in contrast, when predation is dominated by ground

72   predators, birds will place nests at greater height from the ground (Jara et al. 2019). Another

73   factor that we consider in this hypothesis is canopy cover. Some aerial predators search for prey

74   while perched in the canopy. Hence in habitats dominated by aerial predators that exhibit sit and

75   wait behavior, we predict that passerine birds will place nests in sites where there is less canopy

76   cover and/or where the canopy is taller (both factors, will effectively put raptors farther away

77   from nests placed in the understory).

78   Hight-latitude forests offer ideal natural laboratories because they have a simpler

79   structure compared to tropical forests (Rozzi et al. 2014). Consequently, sub-Antarctic forests of

80   South America provide unique opportunities to test the total-foliage and predator proximity

81   hypotheses and collect evidence to understand the mechanisms that explain nest-site selection

82   and nest survival. Navarino Island (55°S), located in the Cape Horn Biosphere Reserve, hosts the

83   world's southernmost forests (Rozzi et al. 2012) and serves as the breeding ground to 28 bird

84   species (Ippi et al. 2009, Rozzi 2010). Here, passerines are the most diverse and abundant group

85   of terrestrial vertebrates, due to the absence of herpetofauna and the limited number of native

86   terrestrial mammals (Dardanelli et al. 2014). Hence, nest-site selection takes place in the context

87   of a simple assemblage of vertebrate predators, which until the end of the twentieth century

88   included only diurnal and nocturnal raptors (e.g., *Accipiter chilensis*, *Caracara plancus*,

89   *Glacidium nana*, *Falco sparverius*, *Milvago chimango*, and *Strix rufipes*; Ippi et al. 2009,

90   Schüttler et al. 2009). Among the most common open-cup passerines breeding in these forests

91   are the White-crested Elaenia (*Elaenia albiceps*), Rufous-collared Sparrow (*Zonotrichia*

92   *capensis*), Patagonian Sierra-Finch (*Phrygilus patagonicus*), Austral Thrush (*Turdus falcklandii*),

93   and Tufted Tit-Tyrant (*Anairetes parulus*) (Rozzi and Jiménez 2014). Although abundant across

94   their range (Medrano et al. 2018), little is known about these species regarding their nesting

95   habits and nest survival.

96   In other systems birds prefer to nest in sites with lower risk of depredation by avian

97   predators (Sergio et al. 2003, Roos and Pärt 2004, Latif et al. 2012). On Navarino Island, bird

98   nesting strategies may also be aimed at reducing the risk of depredation by raptors, the top native

99   predators in this ecosystem. Preliminary evidence suggests that, for example, *T. falcklandii* on

100 Navarino Island breeds closer to the ground than mainland populations (Jara et al. 2019) where

101 the predator assemblage includes several terrestrial species such as wild cats and foxes (Zúñiga

102 et al. 2008, Altamirano et al. 2013). However, the simple predator-prey system on Navarino

103 Island, dominated almost exclusively by raptors, was disrupted two decades ago with the

104 introduction of the American mink (*Neovison vison*) (Rozzi and Sherriffs 2003), and the rapid

105 increase of feral domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*) (Rozzi et al.

106 2006b). These three exotic predators actively prey on passerine birds on Navarino Island

107 (Schüttler et al. 2008, 2018), and worldwide (Ferreras and Macdonald 1999, Bartoszewicz and

108 Zalewski 2003, Doherty et al. 2016). Hence, the arrival of these mammals presented a new

109 predation pressure for birds nesting on Navarino Island and may represent an ecological trap for

110 birds that evolved in the absence of terrestrial predators. The increasing abundance of these

111 novel predators during the first two decades of the 21st century coincides with the rapid

112 disappearance from the island of the Magellanic Tapaculo, *Scytalopus magellanicus*, a small

113 passerine with poor flying capacity that inhabits the understory of South American temperate

114 forests (Rozzi et al. 1996). This bird was detected in the Omora Ethnobotanical Park until 2003

115   (Ippi et al. 2009), but not in recent surveys of the area (Rozzi and Jiménez 2014, R Crego, 2015,

116   pers. comm.).

117   According to the total-foliage hypothesis, to reduce the risk of predation, passerines

118   should nest in sites that provide more nest concealment (Table 1). According to the predator

119   proximity hypothesis, passerines should select nest-sites that avoid the presence of predators,

120   thus reducing the risk of predation. Based on these hypotheses, we predict that on Navarino

121   Island birds place nests in sites with denser and taller understory, and will avoid placing nests

122   close to the canopy (exposing them to perched raptors), or too close to the ground (exposing

123   them to recently introduced ground predators) (Table 1). We also predict that survival rates

124   would be lower in nests located at these extremes of the vertical axis of the forest structure. To

125   test these hypotheses, we collected data on forest-dwelling passerines in the world's

126   southernmost forests with two general goals: i) to test the importance of habitat characteristics on

127   nest-site selection, and ii) to determine how habitat characteristics and temporal variables

128   influence daily nest survival rate (DSR). We examined habitat variables that are relevant for nest

129   survival according to the total-foliage and predator proximity hypotheses (Table 2).

130

131   **Materials & Methods**

132   **Study site**

133   The study site is located on the northern coast of Navarino Island (54°S), within the Cape Horn

134   Biosphere Reserve, at the southern end of South America. Its forests encompass a mixture of

135   evergreen and deciduous species dominated by *Nothofagus* spp., and the understory is composed

136   of shrubs and new-growth forest (Rozzi et al. 2014). The regional climate is oceanic, resulting in

137   a mean rainfall of 467 mm homogeneously distributed throughout the year, and in low annual

138   temperature range, with a mean temperature of 10.8°C during warmest month in summer of and

139   1.9°C in the coldest month in winter (Rozzi et al. 2014). We surveyed for nests along 28 km

140   throughout the northern shore forests; however, most of our efforts were concentrated within the

141   more accessible and protected forests in the Omora Ethnobotanical Park (54°56′S, 67°39′W)

142   (Rozzi et al. 2006a).

143

144   **Nest searching and monitoring**

145   We searched for nests during three breeding seasons: 2014 – 2015 (November – January), 2015 –

146   2016 (October – February) and 2016 – 2017 (October – January). We located active nests (under

147   construction or containing at least one egg or young) by observing and following adults

148   exhibiting signs of breeding or nesting behavior (carrying nest material, defending territory via

149   alarm call, or carrying food or fecal sacs in their bills). In cases where we suspected the nest was

150   in a well-delineated small area, but we were unable to see it, we scanned the vegetation with a

151   thermal imaging camera (FLIR One, 2014 © FLIR® Systems, Inc.) to help locate the nest. We

152   monitored active nests until young fledged or the nest failed, using both camera traps (Bushnell

153   Trophy Cam: Bushnell Corp., Overland Park, KS, USA) and nest visitation. We deployed a

154   camera trap between 1 – 3 m from the nest, depending on the surrounding vegetation. We set

155   cameras to take three consecutive pictures per trigger (to increase chances of detecting the

156   predator) and set a minute delay between triggers. We did not deploy cameras during the laying

157   and early incubation period to prevent nest abandonment (Pietz and Granfors 2000). About 10%

158   of nests did not have cameras deployed at any stage. We typically visited nests every other day,

159   unless we suspected a possible change of nest developmental stage (i.e., laying, incubation,

160   nestling), in which case we visited them every day. During our nest visits, we verified that no

161   predators were in the vicinity to observe our movements and later prey on the nest. Otherwise,

162   we did not approach the nest at that time. We considered a nest successful if: i) the nest was

163   empty and there were fledglings near it, ii) the camera detected them leaving the nest in the

164   absence of predators, and/or iii) the nest was empty and there was fecal matter on the rim of the

165   nest or underneath it. We considered a nest to have failed if: a) there were dead nestlings on or

166   around it, b) it was empty (either intact or destroyed) before the earliest possible date of fledging,

167   or c) the eggs never hatched and there was no adult activity (i.e., abandoned during incubation).

168

169   **Nest site characteristics**

170   After nesting ended we characterized the nest site following a modified BBIRD protocol (Martin

171   et al. 1997). We measured habitat features that might influence the presence of predators and

172   their ability to find nests, including potential perching substrate for raptors, and features that

173   contribute to nest concealment. Within a 5-m radius plot, centered on the nest, we recorded nest

174   height from ground (cm) (hereafter nest height, measured to the rim of the nest), mean nest

175   coverage (%) (hereafter, concealment, estimated as the mean nest coverage measured from 1 m

176   above the nest and from each cardinal direction), canopy cover (%), canopy height (m),

177   understory cover (%), and understory height (cm). We also visually estimated a ground predator

178   (i.e., American mink, rodents, dogs, and cats) accessibility index for every nest. This index

179   ranged from $0 - 2$ with 0 indicating nests that were difficult for a ground predator to access (i.e.,

180   nest placed high in a tree without easily accessible branches from the ground), 1 indicating nests

181   that could be accessible from the ground (i.e., nest above ground level but of easy access for a

182   ground predator through climbable branches), and 2 indicating nests that were placed on the

183   ground and could have been easily accessed by potential ground predators.

184   We assessed nest site selection by measuring the same habitat characteristics (except

185   those specifically related to the nest) using a paired random plot for each nest. Each random plot

186   was located at a random direction and random distance between 25 – 70 m from the nest. We

187   chose this distance to maximize the chances the plot was within the home range of the breeding

188   pair. However, because there is no information of home range sizes for these species, these

189   distances are based on personal observations during the study. Before we measured habitat

190   characteristics at the random paired plot, we verified that active nests of these species were not

191   present at the plot.

192

193   **Statistical analyses**

194   *Nest-site selection*. We used logistic regression to investigate whether habitat characteristics

195   influenced nest-site selection. We developed separate candidate models for each species to assess

196   the probability that a plot contained a nest as a function of canopy cover, canopy height,

197   understory cover, and understory height (Table 1). The response variable was either 1 or 0,

198   indicating presence or absence of a nest, respectively. We ran these four univariate models, as

199   well as all possible combinations of variables, excluding interactions, and estimated their Akaike

200   information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). We

201   selected the top model as the one having the lowest AIC_c, and evaluated parameter importance

202   by determining whether or not their 95% confidence interval (CI) included zero (Tabachnick and

203   Fidell 2001). We considered a parameter to be important if their 95% CI did not include zero.

204   Before fitting the models, we checked for outliers with Cook's distance (D), and for correlation

205   among covariates ($r > 0.75$). For *T. falcklandii* there was one outlier for understory height

206   (Cook's D > 1). Replacing this value with the mean of the variable produced similar results as

207   the original value. Furthermore, this variable did not have a meaningful effect on the response

208   variable (see Results). Therefore, we conducted the analysis with this outlier in the data. We used

209   χ^2 tests to determine goodness of fit of the final models, accepting the model if $p > 0.05$. We

210   calculated the odds ratio to determine the effect of significant habitat predictor variables on the

211   likelihood of a plot containing a nest.

212

213   *Nest survival*. We used the logistic exposure method (Shaffer 2004) to investigate temporal and

214   habitat variables that influenced daily nest survival rate (DSR) by species (Table 2). We

215   evaluated alternative models using a two-stage process. First, we evaluated temporal variables:

216   nest age (days since first egg was laid; linear vs quadratic effects), nest stage (egg [laying and

217   incubation] vs nestling), and day of year (linear vs quadratic effects). We used the best model

218   from this first stage (the one with lowest AIC_c) as the starting model and evaluated habitat

219   variables in the second stage: concealment, canopy cover, canopy height, understory height,

220   understory density, nest height (linear vs quadratic effects), and ground predator accessibility

221   index. From the second stage, we selected the model with lowest AIC_c as the final model for

222   each species. We evaluated the importance of each parameter in the final model by determining

223   whether or not their 95% confidence interval (CI) included zero (Tabachnick and Fidell 2001).

224   For both stages, we built candidate models using all possible combinations of variables,

225   excluding interactions. Finally, we assessed the goodness of fit of the final models with χ^2 tests,

226   accepting the model if $p > 0.05$. We estimated overall nest survival with the final DSR model for

227   every species, holding continuous variables at their standardized mean value ($\bar{x} = 0$). For models

228   with categorical variables, we estimated a separate DSR for each level of the variable(s). To

229   estimate total survival we raised DSR to an exponent equal to the average number of risk days

230   (i.e., either per nesting stage or whole nesting cycle) per species.

231   For the two species with more nests (*E. albiceps* n = 27 and *Z. capensis* n = 35) we used

232   generalized linear mixed models (R package lme4 v1.1.18.1; Bates et al. 2015), using breeding

233   season as a random factor to control for annual differences. For the other three species (*P.*

234   *patagonicus* n = 16*, T. falcklandii* n = 7, and *A. parulus* n = 14), sample size was insufficient for

235   mixed model convergence. Therefore, we used generalized linear models (R Developement Core

236   Team 2018) and excluded breeding season from the analysis, which was correlated with ground

237   predator index for these three species. Furthermore, in a prior analysis we determined that

238   breeding season did not have a meaningful effect on DSR for any of these three species. We

239   checked for outliers with Cook's distance, correlation among continuous variables ($r > 0.75$), and

240   correlation among categorical variables (assessed with a χ^2 test $p < 0.05$). For *T. falcklandii* there

241   was one outlier for concealment (Cook's D > 1) that did not affect model results. Therefore, we

242   conducted all the analysis with this outlier in the data. The only significant correlation among

243   covariates was between canopy height and understory height ($r = -0.97$) for *T. falcklandii*. We

244   included understory height in the candidate models because it would be easier to measure in the

245   field for future studies. For *Z. capensis,* we only evaluated explanatory variables for nests that

246   were on the ground because all three nests above the ground were successful (there was quasi-

247   complete separation of data points). We replaced missing values with the mean of the variable

248   (Acock 2005). Across species and variables, 2.6% of exposure periods — the time between nest

249   visits — had missing values. All continuous variables were standardized to a mean of zero with

250   one unit of standard deviation for analysis (Schielzeth 2010).

251   Before we fit nest survival models for each species, we evaluated the potential for a

252   researcher effect on DSR based on camera deployment and nest visitation. Deploying a camera

253   and/or visiting a nest could negatively affect DSR because parents could abandon their nests due

254   to the disturbance. To evaluate the effect of camera presence, we incorporated an indicator

255   variable where 1 = nests with a camera for that exposure period, and 0 = nests without a camera

256   for that exposure period. To evaluate the effect of visits on DSR we created a continuous

257   variable of cumulative number of visits. For this, we assumed that the effect of visiting a nest

258   was delayed (it occurred after we left the nest) and it was higher the more times we visited a nest.

259   If either camera or visit effect were significant we kept the variable(s) in the final model. All

260   analyses were performed in R 3.5.1 (R Developement Core Team 2018).

261

262   **Results**

263   **Nest-site selection**

264   We located 104 nests for the five species during three breeding seasons (*E. albiceps* n = 28, *Z.*

265   *capensis* n = 35, *P. patagonicus* n = 17, *T. falcklandii* n = 8, and *A. parulus* n = 16). Nest-site

266   habitat characteristics varied both within and among species (Table S1). Understory cover

267   positively influenced nest-site selection in three of the five species (*Z. capensis*, *P. patagonicus,*

268   and *A. parulus*) (Figure 1 and Table 3). The odds of a plot containing a nest of any of these three

269   species increased by a factor of 1.03 with every 1% increase in understory cover. Conversely,

270   this parameter negatively influenced nest-site selection for *E. albiceps*; however, its 95% CI

271   overlapped zero (Table 3). Understory height positively influenced nest-site selection of *P.*

272   *patagonicus* (Figure 1 and Table 3). Finally, although the final nest-site selection model of *A.*

273   *parulus* had understory height and canopy height in it, both of these parameters had their CI

274   overlapped zero (Table 3). The models provided a good fit for the data (Table S2). For *T.*

275   *falcklandii*, the best model was the null model (Table 3), indicating that none of the habitat

276   characteristics were predictive of nest location. For a complete list of competing nest-site

277   selection models, see Table S3.

278

279   **Nest survival**

280   Of the 98 nests monitored that had a known fate, 52% of them failed (n = 51). The success rate

281   per species was: *E. albiceps* 33% (n = 18), *Z. capensis* 44% (n = 34), *P. patagonicus* 63% (n =

282   16), *T. falcklandii* 43% (n = 7), and *A. parulus* 71% (n = 14). Of the 51 failed nests, 71% (n =

283   36) were due to predation. However, we were unable to identify the predator for 58% (n = 21) of

284   the predation events (either the nest did not have a camera or the camera failed to capture the

285   event). We only identified three predators in the system: *M. chimango*, *N. vison* and *Glaucidium*

286   *nana*, which accounted for 13 (87%), 1 (7%), and 1 (7%) of the predated nests we were able to

287   identify the predator, respectively. *Milvago chimango* mostly predated nestlings, whereas the

288   latter two predated eggs. Most predation events (69%) occurred during the nestling stage. Nest

289   abandonment accounted for the remaining failed nest (n = 15). *Elaenia albiceps* and *T.*

290   *falcklandii* had the highest abandonment rate, 26% (n = 7) and 29% (n = 2), respectively. In

291   contrast, *P. patagonicus* and *A. parulus* abandoned 0% and 7% (n = 1) of their nests,

292   respectively. *Zonotrichia capensis* abandoned 15% (n = 5) of its nests. Most abandonments

293   (80%, n = 12) occurred during the incubation stage.

294   There was no evidence that researcher visitation affected nest daily survival rate (DSR)

295   for any species. Thus, we examined the influence temporal and habitat variables without

296   considering the effect of our visits. *Zonotrichia capensis* was the only species where camera

297   presence affected DSR; DSR increased by 22% when a camera was present ($\widehat{\text{Œ} =}$ = 1.97; 95%

298   CI = 0.20 - 3.61; Figure 2). Thus, for this species only, we proceeded with model selection by

299   including a camera effect. Overall nesting success, based on DSR, was highest for *P.*

300   *patagonicus* (87.0%) and *A. parulus* (99.9%), although the latter had a much larger CI (Figure 3).

301   The lowest overall nesting success was 1.4%, corresponding to the egg (i.e. laying + incubation)

302   stage in the absence of camera for *Z. capensis* (as camera presence significantly affected DSR for

303   this species; Figure 3).

304   For the best supported model of *E. albiceps*, we found that there was a non-linear effect

305   of nest age on DSR; survival rate was high except for a decline 5 days after hatching (Figure 4)..

306   Also, DSR declined with increasing canopy cover and understory height (Figure 4). In addition,

307   DSR declined with increasing concealment, however, the CI for this variable overlapped zero

308   (Table S4). For *Z. capensis,* in addition to the camera effect, DSR was strongly influenced by

309   nest age (Figure 2). DSR was lowest around 8 days after hatching, but high at the beginning and

310   end of the nesting period (Figure 2A). DSR followed a similar pattern in the presence or absence

311   of a camera, although survival did not decrease as much in nests with camera (Figure 2A).

312   Nestlings had a higher probability of surviving than eggs (Figure 2). Eggs' DSR was 26.8% and

313   1.4%, in the presence and absence of camera, respectively. Nestlings' DSR was 89.2% and

314   45.0%, in the presence and absence of camera, respectively (Figure 3). DSR of *P. patagonicus*

315   declined slightly with increasing nest age, understory cover, and understory height, and it

316   strongly increased with more nest concealment (Figure 5). For *T. falcklandii,* DSR declined with

317   increasing understory cover (Figure 6). Finally, DSR of *A. parulus* was influenced by a non-

318   linear effect of nest age; DSR was lowest around 8 days after hatching, but high otherwise. Also,

319   DSR increased with nest height and understory cover. However, CIs for all variables in the final

320 model for this species overlapped zero (Table S4). The best supported model for every species

321 were good fits for the data (Table S2). For details on parameter estimates and CIs of the best-

322 fitted nest survival models for each species, see Table S4. For a list of competing nest survival

323 models, see Table S5.

324

325 **Discussion**

326 Our study provides new evidence that nest survival is influenced by predation. In addition to

327 support previous studies that have found similar effect (Nice 1957, Ricklefs 1969, Liebezeit and

328 George 2002, Bellamy et al. 2018, Reidy and Thompson 2018), we propose a novel hypothesis

329 that combines characteristics of the *habitat* where the nest is built (canopy height, canopy cover,

330 understory height, understory cover – total-foliage hypothesis) and of the *habits* of potential and

331 actual predators (attack mode of aerial vs terrestrial predators - predator proximity hypothesis)

332 that influence (a) nest-site selection and/or (b) nest survival (breeding success).

333

334 **(a) Nest-site selection**

335   We found percentage of understory cover was the most important habitat variable

336 explaining nest-site selection, as it affected three of the five species. *Zonotrichia capensis*, *P.*

337 *patagonicus* and *A. parulus* significantly preferred nesting sites with greater percentage of

338 understory cover (Figure 1). In addition, *P. patagonicus* preferred to nest in sites with taller

339 understory (Figure 1). This finding is consistent with the total-foliage hypothesis, which assumes

340 that more foliage reduces the risk of depredation because it interferes with visual, auditory, and

341 olfactory cues for avian and mammalian nest predators (Martin and Roper 1988, Martin 1993).

342 Our findings for these three species are also consistent with previous studies on North American

343   passerines, where species placed their nests in higher understory density and/or cover compared

344   to non-nest random plots (Liebezeit and George 2002, Benson et al. 2009, Wynia 2013).

345   The other two passerine species, *E. albiceps* and *T. falcklandii*, selected nest sites with

346   characteristics that were no different from random paired plots. There are at least, two possible

347   explanations for this lack of effect. First, there is a pattern that we were unable detect. Among

348   the five species studied, *E. albiceps* and *T. falcklandii* exhibit the highest diversity of substrates

349   used for nesting (Jara et al. 2019). In addition, *E. albiceps* and *T. falcklandii* nest at the high and

350   low extremes of the vertical forest profile (Jara et al. 2019). The high heterogeneity of nesting

351   substrate and position in the vertical axis of the forests could make it more complex to detect a

352   pattern. Second, birds could be using an unstructured pattern for nest placement to deter

353   predators from learning to scan for nests. This has been suggested for Hermit Thrush (*Catharus*

354   *guttatu*; Martin and Roper 1988) and White-tailed Ptarmigan in North America (*Lagopus*

355   *leucurus*; Wiebe and Martin 1998). This mechanism could also provide an explanation for the

356   lack of significant association between nest-sites and the other two examined habitat variables

357   (canopy height, canopy cover) in the five studied passerine species. More research with larger

358   sample sizes is needed to elucidate this potential explanation for predator avoidance.

359

360   **Nest survival**

361   Overall survival rates were high for *P. patagonicus* (87.0%), *T. falcklandii* (67.2%), and *A.*

362   *parulus* (99.9%) (Figure 3). Nest survival rate recorded for *T. falcklandii* in the remote sub-

363   Antarctic forests on Navarino Island is much higher than the 20% that have been recorded for

364   conspecific populations in temperate forests further north in southwestern Patagonia on Chiloé

365   Island (42°S), Chile (Willson et al. 2014). In contrast, survival rates were low for *E. albiceps*

366 (31.0%) and *Z. capensis* (1.4 – 89.2% depending on camera presence and nest stage; Figure 3).

367 The low rates we found for these two species are similar to the rates found for conspecific

368 populations of *E. albiceps* breeding on Chiloé Island, Chile (27% of nest success) (Willson et al.

369 2014), and of *Z. capensis* breeding on central Monte Desert, Argentina (34°S; 9.4% of nest

370 success) (Mezquida and Marone 2001). On Navarino Island, *T. falcklandii* builds its nests closer

371 to the ground than further north in the temperate forest biome (Jara et al. 2019). This could be

372 associated with the fact that mammalian ground predators are present in temperate forests, but

373 until recently, were absent on Navarino Island (Jara et al. 2019). Could the difference in

374 proximity to prevailing predators explain the differences in nest-placement and nest survival in

375 *T. falcklandii* at different latitudes? Can the historical absence of ground mammal predators and

376 the presence of aerial bird predators on Navarino Island explain the high survival rates of *P.*

377 *patagonicus*, *A. parulus*, *T. falcklandii*? Why do the nest-survival rates of these species differ

378 from the low rates detected for *E. albiceps* and *Z. capensis*?

379   The main cause of nest failure (71%), regardless of species, was predation. This is

380 consistent with passerines breeding in northern hemisphere forests (Ricklefs 1969, Murphy 1983,

381 Martin 1993, Wilson and Cooper 1998, Duguay et al. 2001, Liebezeit and George 2002,

382 Wesolowski and Tomialojc 2005). On Navarino Island, the native raptor *M. chimango* was the

383 most common predator, accounting for 87% of the depredated nests where we were able to

384 identify the predator; corresponding with previous studies on this island (Ibarra 2007, Schüttler

385 et al. 2009, Maley et al. 2011, Crego 2017). On Chiloé Island, farther north within the south-

386 temperate rainforest, *M. chimango* is also the main predator of passerine nests (Willson et al.

387 2001).

388   *Milvago chimango* is a common raptor in southern South America that inhabits a variety

389   of habitat types, including forests, shrub-lands, steppes, coastal ecosystems, as well as

390   anthropogenic habits such as plantations and cities (Rozzi et al. 1996). This opportunistic raptor

391   is a generalist predator that uses a wide variety of foraging techniques. It can fish using 'glide-

392   hover' technique, catch fleeing insects while flying through fires, or wade to catch frogs and

393   tadpoles (del Hoyo et al. 1994, Sazima and Olmos 2009). In the forests of Navarino Island, it

394   mostly searches for prey while perched and flying overhead (R.F. Jara and R.D. Crego personal

395   observation). On Navarino Island *M. chimango* also predates nests irrespective of their height

396   from the ground (Crego 2017). Consequently, it exerts a predation pressure from above (like

397   other raptors) and from below (like ground predators). This suggests that birds on this island may

398   have already developed nesting strategies to avoid ground predation pressure, even before

399   mammal ground predators were introduced. It is important to consider that *M. chimango*

400   populations increase with human disturbance, like those generated on Navarino Island during the

401   last couple of decades by the king-crab industry dumping large quantities of shellfish

402   exoskeleton that attract this bird. Thus, this may represent an ecological trap, because birds on

403   this island evolved under different historical and current predator abundance conditions

404   (Chalfoun and Schmidt 2012). For the reasons discussed above, we recommend monitoring

405   population growth and subsequent impact of *M. chimango* on nesting passerines in the Cape

406   Horn Biosphere Reserve.

407   The only ground mammal predator we identified was *N. vison,* which depredated 7% of

408   nests with a known predator. This semi-aquatic mustelid was introduced to Navarino Island at

409   the end of the 20th century (Rozzi and Sherriffs 2003) and is known for its negative impacts on

410   native birds on Navarino Island (Schüttler et al. 2008, 2009, Maley et al. 2011), and worldwide

411 (Ferreras and Macdonald 1999, Nordström and Korpimäki 2004, Bonesi and Palazon 2007,

412 Brzeziński et al. 2012). However, and contrary to our expectations, its nest depredation rate on

413 passerines was very low. A possible explanation could be a mismatch between the periods of *N.*

414 *vison's* peak activity in the forest (summer) (Crego 2017) and the onset of passerine nesting

415 season (Spring) (Jara et al. 2019). Alternatively, because we were unable to identify the predator

416 in 58% of the events, we may have underestimated the effect of this mustelid — and other

417 potential predators such as feral cats and dogs — on nest survival, as birds are part of the *N.*

418 *vison* and cat diets (Schüttler et al. 2008, 2018). Contrary to previous findings on artificial nests

419 (Willson et al. 2001, Maley et al. 2011), we found no evidence of nest predation by rodents or

420 House Wrens (*Troglodytes aedon*). This may be because in our study of natural nests, parents

421 can actively deter rodents and/or House Wrens (Jara et al *in prep*).

422   Nest-site selection was positively influenced by higher percentage of understory cover

423 (*Z. capensis, P. patagonicus,* and *A. parulus*) and taller understory (*P. patagonicus*) (Table 3).

424 However, for *Z. capensis* and *A. parulus*, understory cover and understory height did not have an

425 effect on nest survival. Furthermore, for *P. patagonicus,* these two habitat characteristics had an

426 opposite effect, negatively influencing DSR (Figures 4C, 5B, 5C, and 6A). Thus, it seems that

427 these species are selecting nest-sites that not only have a neutral effect on nest survival, but

428 actually decrease their survival rates. Given that predation was the main cause of nest failure, it

429 is possible that there is a disconnect between birds assessing the risk of predation (and selecting

430 the appropriate nest-site) and the actual risk of predation. This could be attributed to an

431 ecological trap. The potential increase of *M. chimango* abundance associated with urban

432 development could be changing historical conditions of predator assemblage. Furthermore,

433 passerine populations on this island have evolved with a different predator assemblage (i.e., only

434   aerial predators), but this has been disrupted with the introduction of exotic ground mammal

435   predators to this island, and the rapid increase of feral domestic cats and dogs, less than 20 years

436   ago. This ecological trap would imply a delay in the ability of birds to adapt nesting behavior in

437   response to a new type and or abundance of predators. Alternatively, the mismatch between nest-

438   site selection and DSR could also be due to methodological problems (e.g., limited sample size,

439   wrong choice of habitat variables, etc.), or ecological-evolutionary reasons (e.g., tradeoffs with

440   other selection pressures such as microclimate and access to food, etc.) (reviewed by Chalfoun

441   and Schmidt 2012). Further research will be needed to assess hypotheses that could explain this

442   mismatch between nest-site selection and nest survival.

443   For two of the three species in which we found a nest age effect on DSR (*E. albiceps*, *Z.*

444   *capensis*, and *P. patagonicus*), the pattern was similar (i.e., quadratic effect) even though its

445   magnitude varied considerably (Figures 2A and 4A). The low rates of nest failure during the

446   laying and incubation periods suggest marginal effects of nest abandonment and depredation by

447   *M. chimango* and *N. vison* (the only two identified predators during these nest stages) during the

448   first half of the nesting cycle. Daily survival rates were lowest soon after hatching (Figures 2A

449   and 4A). This may reflect the sudden increase in cues to predators coming from nestlings (visual,

450   auditory, and olfactory) and parents (visual and auditory, as their nest visitation frequency

451   suddenly rises) (Cresswell 1997, Martin et al. 2000, Grant et al. 2005), which increases their

452   vulnerability to predation. After reaching its lowest rate after hatching, nest survival increased

453   steadily during the nestling period (Figures 2A, and 4A). This pattern, which has previously been

454   observed in passerines (Pietz and Granfors 2000, Grant et al. 2005), could be due to increased

455   parental nest defense as nestlings get closer to fledging (Montgomerie and Weatherhead 1988).

456   This is particularly relevant for these five species on Navarino Island, as they only have one

457 brood per breeding season (Jara et al. 2019), and therefore have a greater incentive to protect

458 their nest as young near fledging. Another non-exclusive explanation includes 'forced-fledging'

459 of nestlings by potential predators (Pietz and Granfors 2000). Nestlings that are close to fledging

460 age may avoid depredation by leaving the nest prematurely when they are at imminent risk of

461 depredation. This behavior may decrease depredation-induced nest failures towards the end of

462 the nesting cycle.

463   Higher nest concealment for *P. patagonicus* increased its nesting success (Figure 5D),

464 which is consistent with the total-foliage hypothesis (Martin and Roper 1988, Martin 1993).

465 According to this hypothesis, predators have a harder time locating nests with higher

466 concealment, because it may be harder to detect them visually, aurally, and/or olfactorily. It has

467 been suggested that *M. chimango* can detect nests visually (Crego 2017), so it seems *P.*

468 *patagonicus* may be trying to avoid being detected by nest predators in this system. The parental

469 behavior of this passerine may also be an important contributing factor. *Phrygilus patagonicus*

470 sits still on the nest in response to the presence of a predator, unlike what we observed for the

471 other species, which flush considerably sooner and exhibit alarm behaviors (R.F. Jara personal

472 observation). In the other species, higher nest concealment may not improve nesting success due

473 to their more agitated parental behavior that, in contrast to *P. patagonicus,* may counteract any

474 concealment advantage.

475   We found that higher percentage of canopy cover above nests of *E. albiceps* decreased

476 their nest survival (Figures 4B). This is consistent with the predator proximity hypothesis where

477 nests at higher risk of predation (i.e., aerial or ground) should have lower survival. More canopy

478 cover allows for the presence of *M. chimango*, the most common nest predator we were able to

479 identify, because this forest raptor not only nests in the canopy, but also uses branches in the

480 canopy to perch and look for prey (R.F. Jara and R.C. Crego personal observation). Thus,

481 passerines breeding in areas with more canopy cover may be at higher risk of depredation by this

482 raptor, due to its greater presence in covered areas.

483

484 **Camera effect on nest survival**

485 We found evidence that for *Z. capensis*, the presence of a camera increased DSR by 22%. This

486 positive camera effect has been reported for other bird species or systems (Thompson III et al.

487 1999, Buler and Hamilton 2000, Pietz and Granfors 2000, Small 2005, reviewed by Richardson

488 et al. 2009). Cameras may have a deterrent effect on predators, possibly through neophobia

489 towards these devices, which would consequently reduce predation of these nests. However, this

490 is unlikely to be the case for our study system because *M. chimango* was the main nest predator

491 across all five species, but we only found a camera effect for *Z. capensis*. This suggests *M.*

492 *chimango* did not exhibit neophobia towards the cameras. Furthermore, this raptor has been

493 described as having low neophobia (Biondi et al. 2010). Alternatively, there could be a bias

494 introduced by delaying the camera deployment until later in the nesting cycle. Nests that failed

495 earlier in the cycle, when the camera was absent, may then positively bias our estimates of DSR

496 for nests with a camera later in the cycle. Finally, and possibly a more likely explanation, this

497 result was an artifact of limited exposure periods without cameras (i.e., 7.7%; n = 83/1077).

498

499 **Conclusions**

500 This study provides the first evidence on nest-site selection and survival of open-cup-nesting

501 passerines in sub-Antarctic forests. We also propose a novel hypothesis that represents a

502 relationship between the habitat and type of predators. Although our study was conducted on a

503   single location, this hypothesis could be tested for nest-site selection and nest survival in other

504   regions. We found that the studied bird species selected nest-sites with more understory cover

505   and taller understory, which according to the total-foliage hypothesis would provide more

506   concealment against predators. However, more understory cover and taller understory decreased

507   nest survival. There seems to be a disconnect between birds assessing the risk of predation (and

508   selecting the appropriate nest-site) and the actual risk of predation, resulting in birds selecting

509   riskier sites for nesting. This could be attributed to an ecological trap, were birds on this island

510   evolved with a different predator assemblage, which has been disrupted with the introduction of

511   exotic ground mammal predators to this island, and/or the increased abundance of native *M.*

512   *chimango* associated with urban development. Further research will be needed to assess

513   hypotheses that could explain this mismatch between nest-site selection and nest survival.

514

520

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Table 1(on next page)

Variables incorporated into candidate models assessing habitat characteristics influencing nest-site selection by five forest passerines on Navarino Island, Chile.

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Variable	Hypothesis	Predictions	Rationale
Canopy cover	Predator proximity	Negatively associated with nest presence	More canopy cover allows for the presence of aerial predators, imposing a threat to nesting birds and their nests.
Canopy height	Predator proximity	Positively associated with nest presence	Higher canopy puts perched raptors farther away from birds nesting in the understory, making it harder to detect bird breeding activity.
Understory cover	Total-foliage	Positively associated with nest presence	More understory cover provides more visual nest concealment and interfere with the transmission of odors and sounds coming from the nest that could be detected by a predator.
Understory height	Predator proximity/Total-foliage	Positively associated with nest presence	Taller understory provides more nest concealment against predators, and allows for higher nest placement, which reduces accessibility for ground predators.

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Table 2(on next page)

Justification of variables incorporated into candidate models for estimating daily nest survival rate of five forest passerines on Navarino Island, Chile.

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Model	Variable	Predictions	Rationale
Null	Intercept only	Nest survival is random	Assumes daily survival rate (DSR) is constant.
Temporal effects	Day of year	Negatively associated with DSR	Late nesters will have lower nest survival because of the overlap with increased depredation pressure in the forest interior (i.e. *N. vison*), due to their breeding dynamics.
	Nest age (linear vs quadratic effects) and nest stage	Negatively associated with DSR	Nest age and stage influence adult behavior around the nest (increased nest visitation for food provisioning), and increased noise and odor from nestlings. These cues could be detected by predators.
Habitat effects	Concealment	Positively associated with DSR	Under the 'total-foliage' hypothesis, more nest concealment not only protects the nest and its content from predators, but also the adults entering and leaving it.
	Nest height off the ground (linear vs quadratic effects)	Positively associated with DSR	Under the 'predator proximity' hypothesis, nests closer to the ground will be more susceptible to ground predators
	Ground predator index	Negatively associated with DSR	Under the 'predator proximity' hypothesis, nests with higher index score will be more susceptible to predation.
	Canopy cover, canopy height, understory cover and understory height	Variables associated with nest-site selection will have equivalent effect on DSR.	Rationale of these variables' effect on DSR is equivalent to that described in nest-site selection (Table 1).

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Table 3(on next page)

Parameter estimates (95% confidence interval) for the best model explaining nest-site selection by five forest-nesting bird species on Navarino Island, Chile, 2014-2017.

Species (n)	Coefficients in the best model β (95% confidence interval)		
	Understory cover	Understory height	Canopy height
Elaenia albiceps (22)	-0.13 (-0.298 – 0.004)		
Zonotrichia capensis (33)	0.03 (0.007 – 0.047)		
Phrygilus patagonicus (17)	0.03 (0.003 – 0.054)	0.02 (0.0003 – 0.0423)	
Turdus falcklandii (8)	*	*	*
Anairetes parulus (16)	0.03 (0.003 – 0.059)	0.02 (-0.0001 – 0.0538)	-0.19 (-0.482 – 0.026)

* The final model for this species was the null model

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Figure 1

Probability of nest presence (and 95% CI) as a function of habitat characteristics for three forest-nesting bird species on Navarino Island, Chile, 2014-2017. We only present parameters of the final model for which their CI did not overlap zero.
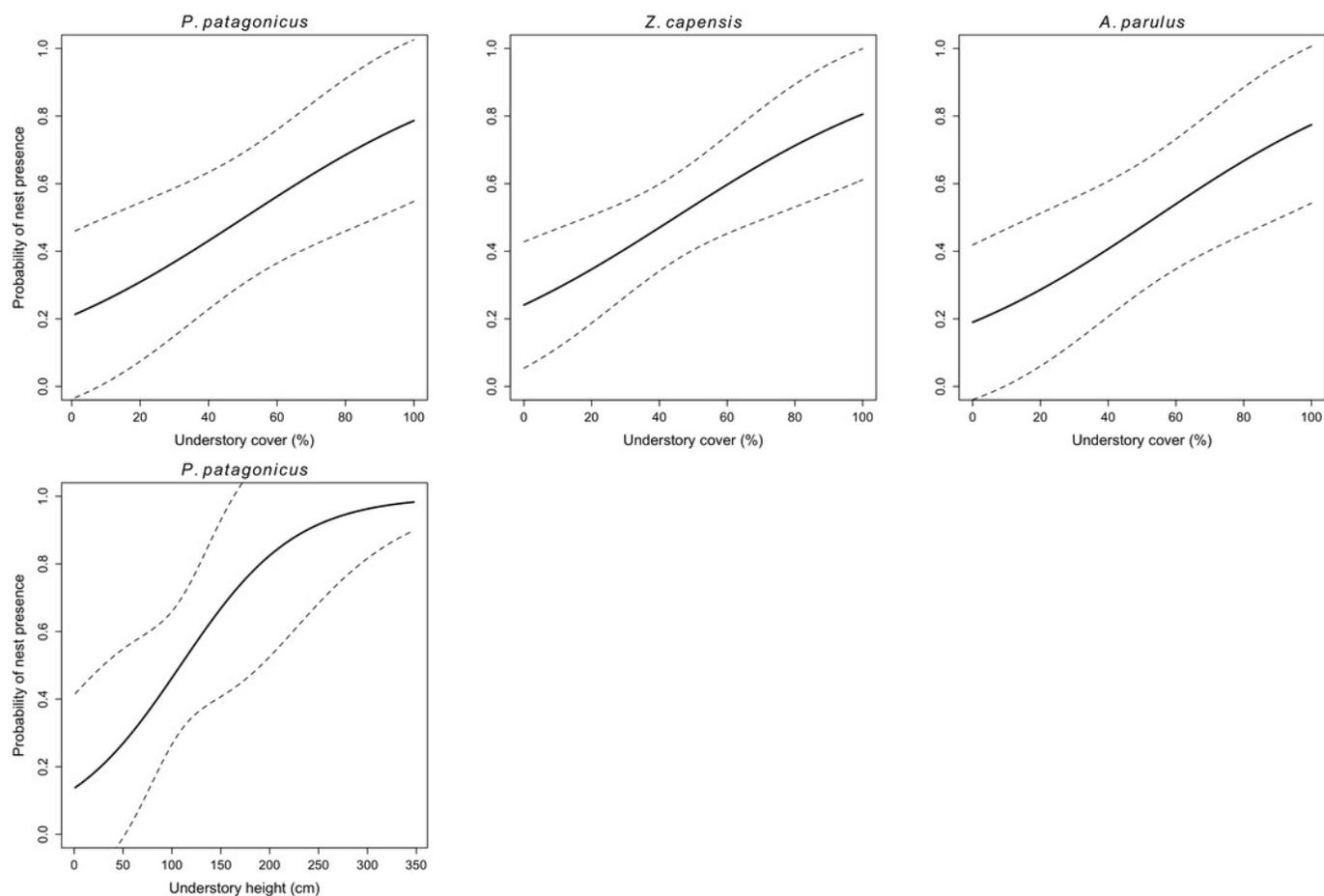
Figure 2

Mean nest daily survival rate (DSR) of *Zonotrichia capensis*

(**A**) Mean nest daily survival rate (DSR) of *Zonotrichia capensis* as a function of nest age and

nest age^2, in the presence and absence of camera. Mean nest DSR was estimated when nest

stage = nestling (1). Dashed line represents mean hatch day for this species (Jara et al.

2019). (**B**) Coefficient estimates (filled circles) for the best model ± their 95% CI (thin-outer

lines) and 50% credible intervals (thick-inner lines).
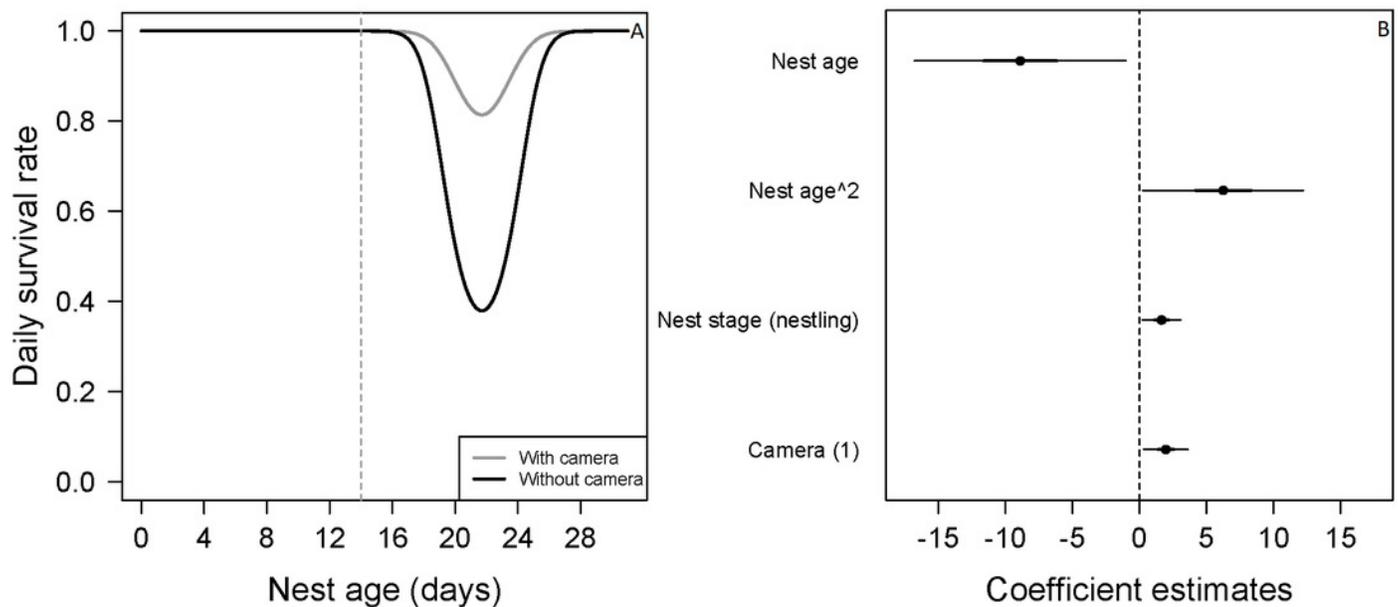
Figure 3

Overall nest survival rate by species

Estimated with the final DSR model for each species, holding continuous variables at their standardized mean value (i.e., 0). Therefore, for models with only continuous variables in it, only one rate was estimated and corresponds to the intercept. For *Z. capensis*, the final model has categorical variables in it (i.e., camera and nest stage). Thus, we estimated separate survival rates for each level of the categorical variable(s), while holding the continuous variables at their standardized mean value of 0. Once we obtained a DSR value, we raised it to an exponent = average # days of the nesting cycle per species (from laying until hatching).
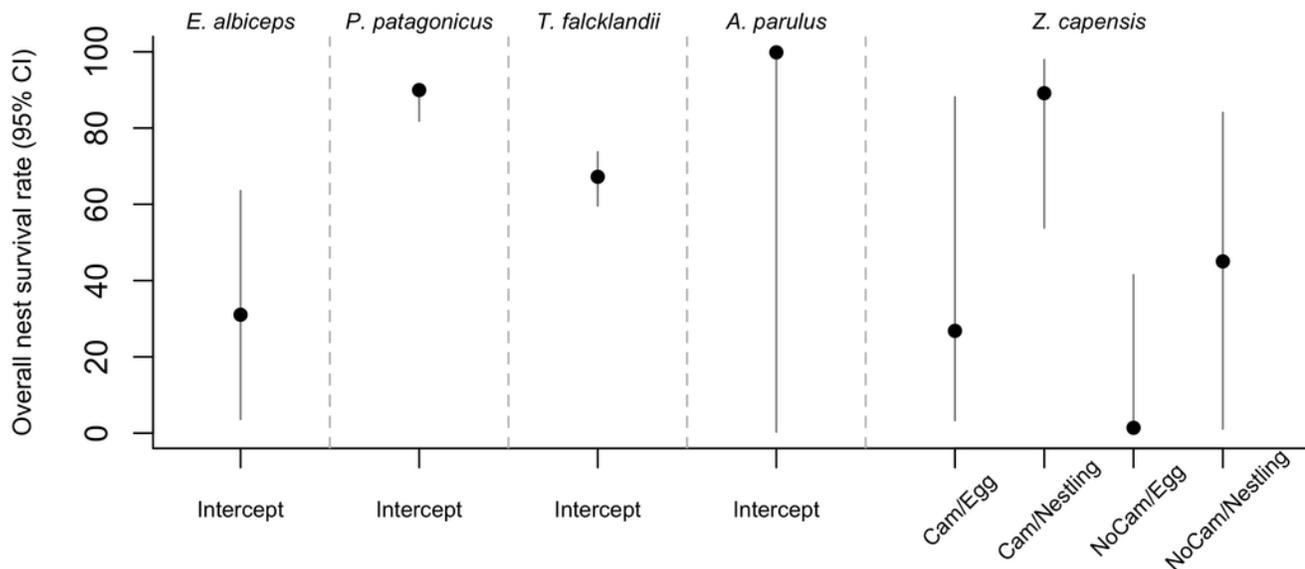
Figure 4

Mean nest daily survival rate (DSR) of *Elaenia albiceps*

(**A**) nest age and nest age^2, (**B**) canopy cover, and (**C**) understory height. Mean nest DSR for each variable estimated holding the other variables at their standardized mean value (i.e., 0). Dashed line in (**A**) represents the average hatch day for this species (Jara et al. 2019). (**D**) Coefficient estimates (filled circles) for the best model ± their 95% CI (thin-outer lines) and 50% credible intervals (thick-inner lines).
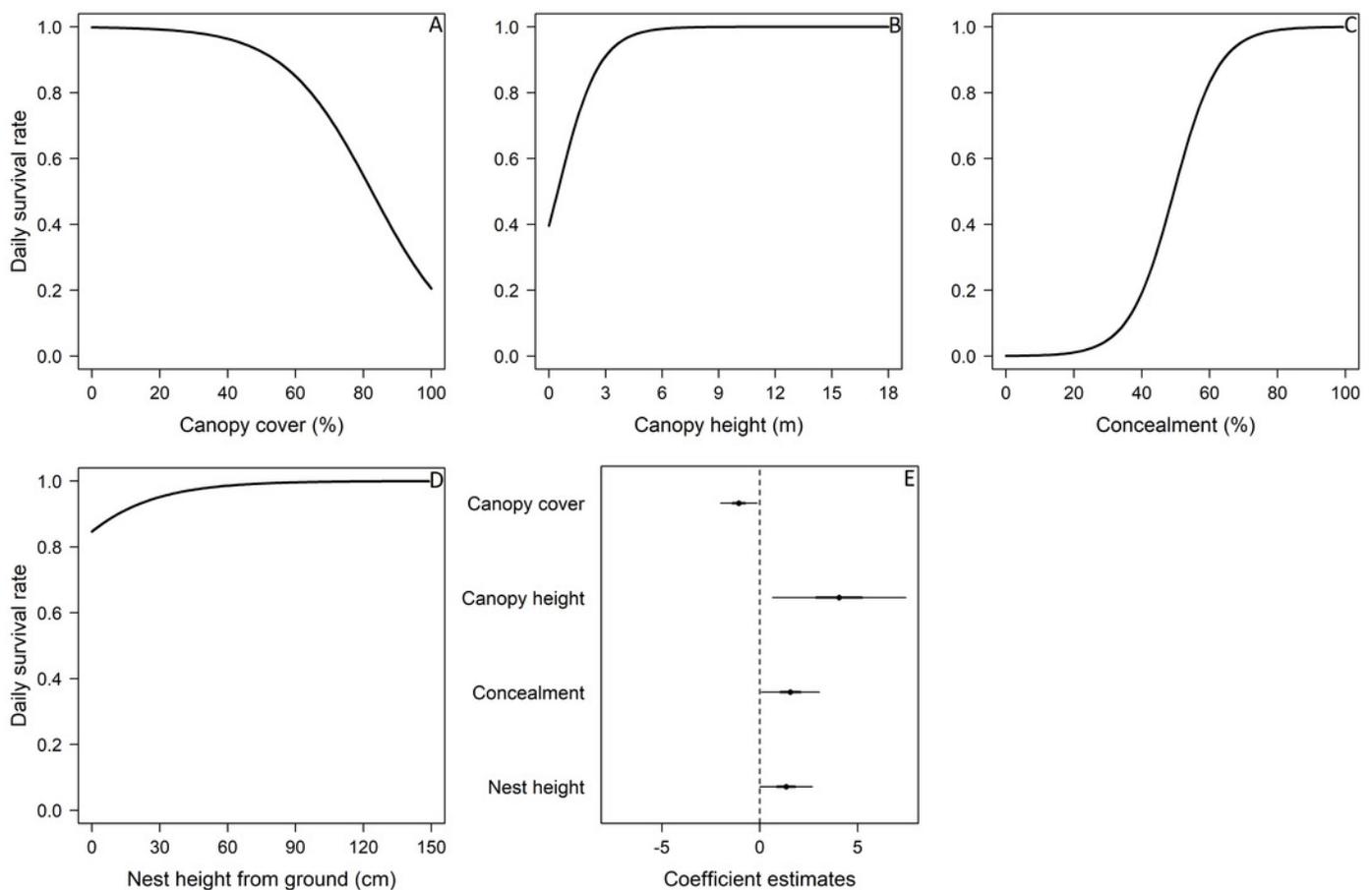
Figure 5

Mean nest daily survival rate (DSR) of *Phrygilus patagonicus*

(**A**) nest age, (**B**) understory cover, (**C**) understory height, and (**D**) concealment. Mean nest DSR for each variable estimated holding the other variables to their standardized mean value (i.e., 0). (**E**) Coefficient estimates (filled circles) for the best model ± their 95% CI (thin-outer lines) and 50% credible intervals (thick-inner lines).
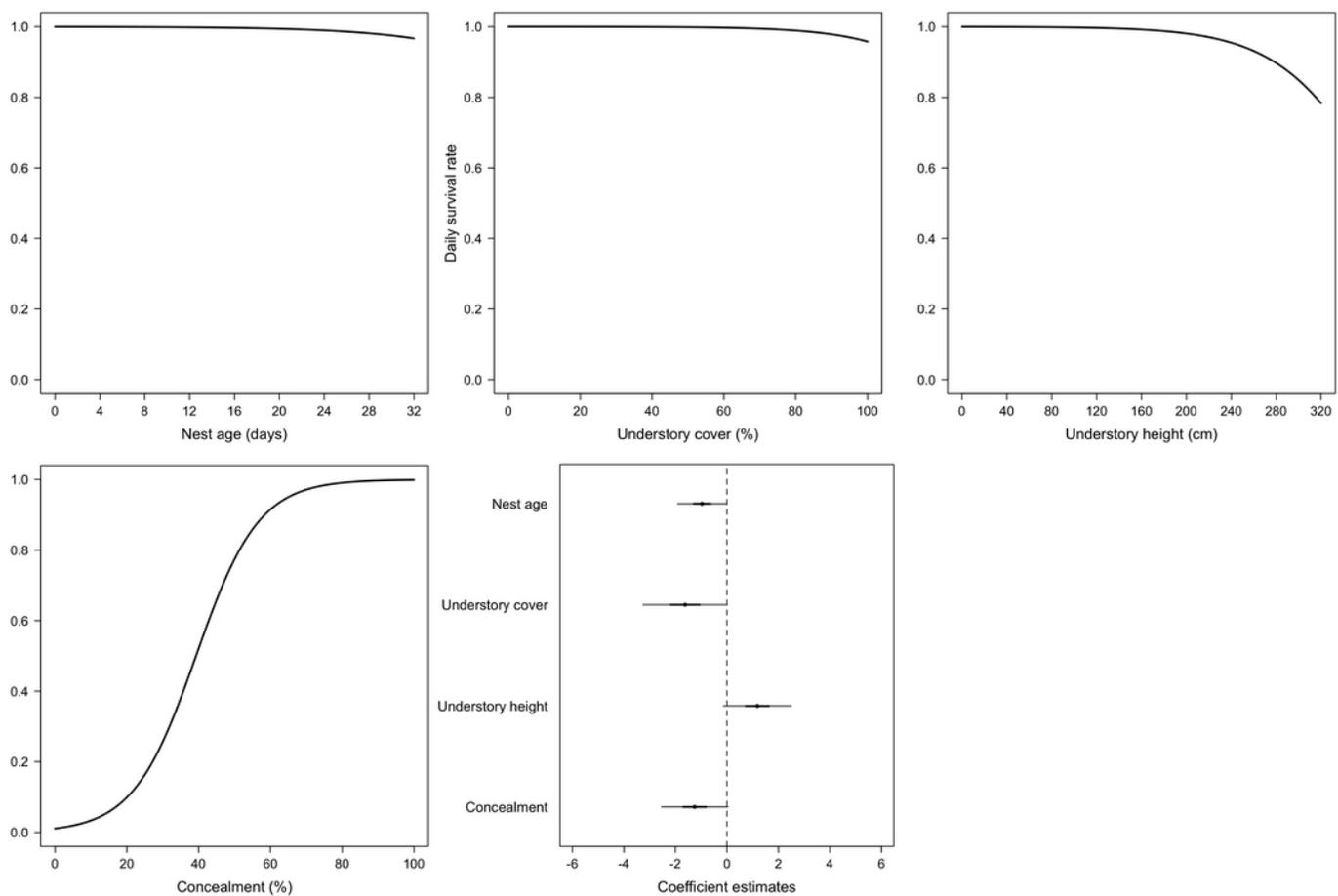
Figure 6

Mean nest daily survival rate (DSR) of Turdus falcklandii

(**A**) understory cover. (**B**) Coefficient estimate (filled circle) for the best model ± its 95% CI
(thin-outer lines) and 50% credible interval (thick-inner lines).