

1 Running head: Woodpeckers as ecosystem engineers

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3 **Secondhand homes: Woodpecker cavity location and structure influences**  
4 **secondary nester's success.**

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6 Faith O. Hardin<sup>1\*</sup>, Samantha Leivers<sup>2</sup>, Jacquelyn K. Grace<sup>3</sup>, David M. Cairns<sup>4</sup>, Tyler Campbell<sup>5</sup>,

7 Brian Pierce<sup>2</sup>, Michael L. Morrison<sup>1</sup>

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9 <sup>1</sup>Department of Rangeland, Wildlife, and Fisheries Management, Texas A&M University,  
10 College Station, Texas, 77843

11 <sup>2</sup>Natural Resources Institute, Texas A&M University, 578 John Kimbrough Blvd, College  
12 Station, Texas, 77843

13 <sup>3</sup>Department of Ecology & Conservation Biology, Texas A&M University, College Station,  
14 Texas, 77843

15 <sup>4</sup>Department of Geography, Texas A&M University, College Station, Texas, 77843

16 <sup>5</sup>East Foundation, San Antonio, Texas, 78216

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19 \*Corresponding Author: Faith.Hardin@tamu.edu

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31 Corresponding Author: Faith Olivia Hardin, E-mail: [faith.hardin@tamu.edu](mailto:faith.hardin@tamu.edu) ORCID:

32 <https://orcid.org/0000-0003-1753-6111>

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## 40 Abstract

- 41 1. Understanding how ecosystem engineers influence other organisms has long been a goal  
42 of ecologists. Woodpeckers select nesting sites with high food availability and will  
43 excavate and then abandon multiple cavities through their lifetime. These cavities are  
44 crucial to secondary cavity nesting birds (SCB) that are otherwise limited by the  
45 availability of naturally occurring cavities.
- 46 2. Our study examined the role food resources have on the nest site location and home range  
47 size of woodpeckers, and the respective influence woodpeckers and the construction of  
48 cavities have on the nesting success of SCB.
- 49 3. Using five years of avian point count data to locate golden-fronted woodpeckers (GFWO:  
50 *Melanerpes aurifrons*), we correlated insect availability with GFWO home range size and  
51 determined differences in insect availability between GFWO occupied and unoccupied  
52 sites, while recording nesting success (success:  $\geq 1$  fledgling) for the GFWO and  
53 common SCB in south Texas: Black-crested Titmouse (*Baeolophus atricristatus*), Ash-  
54 throated Flycatcher (*Myiarchus cinerascens*), Brown-crested Flycatcher (*Myiarchus*  
55 *tyrannulus*), and Bewick's Wren (*Thryomanes bewickii*). We used model averaging to fit  
56 species-specific logistic regression models to predict nest success based on cavity metrics  
57 across all species.
- 58 4. Sites occupied by GFWO had a higher biomass of insects in orders Coleoptera,  
59 Hymenoptera, and Orthoptera than unoccupied sites, and there was a negative correlation  
60 between the availability of these insect orders and home-range size. GFWO had increased  
61 nest success in trees with increased vegetation cover and lower levels of decay, while

62 SCB had higher levels of nesting success in abandoned GFWO cavities opposed to  
63 naturally occurring ones, and in trees with low decay.

64 5. Our results suggest that SCB may be drawn to nest in abandoned woodpecker cavities  
65 where they have higher rates of nest success compared to natural cavities. Additionally,  
66 the prevalence for GFWO to excavate cavities in trees with lower levels of decay  
67 contradicts previous literature and may indicate a novel temperature trade-off, with live  
68 trees requiring more energy to excavate, but providing more protection from high  
69 breeding season temperatures in arid and semi-arid areas.

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79 Key words

80 Ecosystem engineers, secondary cavity nesters, woodpeckers, insect communities, species

81 interactions, nesting success

## 82 1. INTRODUCTION

83 Ecosystem engineers control the availability of resources for other species by causing  
84 physical state changes in biotic or abiotic materials (Jones, Lawton & Shachak, 1994; Wright,  
85 Jones, & Flecker, 2002; Buse et al., 2008). Given the important role they play in local  
86 environments, the literature surrounding ecosystem engineers is historically focused on how their  
87 actions affect other species (Jones et al., 1994; Robles & Martin, 2013; Tarbill, Manley, &  
88 White, 2015; Wiebe, 2017), but little research has been done concerning external factors that  
89 influence the engineers themselves (see Mikusinski, 2006; Jusino, Lindner, Banik, & Walters,  
90 2015). Importantly, little has been done to investigate how ecosystem engineers choose breeding  
91 and young rearing grounds (Nilsson, Johnsson, & Tjernberg, 1991; Garmendia, Cárcamo, &  
92 Schwendtner, 2006). Understanding these driving factors is essential to understanding the  
93 ecology of not only the ecosystem engineers themselves, but the organisms that rely on them for  
94 their own breeding and nesting grounds as well.

95 The modifications made by ecosystem engineers have far-reaching consequences and  
96 directly impact not only ecological associations, but also the behavior of animals within an  
97 ecosystem. For example, animal movement and community composition may be altered by the  
98 actions of local ecosystem engineers (Lill & Marquis, 2003; Bangert & Slobodchikoff, 2004). In  
99 this way, ecosystem engineers can indirectly influence local trophic levels through multi-level  
100 environmental modifications, such as by influencing local invertebrate diversity and abundance,  
101 which in turn may increase foraging opportunities for other vertebrates (Lill & Marquis, 2003;  
102 Bangert & Slobodchikoff, 2004), or by providing more suitable species specific habitat for  
103 nesting (Showalter & Whitmore, 2002)

104           Although insects themselves can act as ecosystem engineers (Bell & Whitmore, 1997;  
105 Lill & Marquis, 2003; Bangert & Slobodchikoff, 2004), they can also act as crucial resources for  
106 other ecosystem engineers at higher trophic levels (Hess & James, 1998; Pechacek & Kristin,  
107 2004). For example, declines in insect richness and abundance have been reported with parallel  
108 declines in a number of insectivorous ecosystem engineers, such as woodpeckers (Lister &  
109 Garcia, 2018, Møller, 2019, Karr, 1976; Benton, Bryant, Cole, & Crick, 2002; Rioux Paquette,  
110 Pelletier, Garant & Bélisle, 2014; Narango, Tallamy, & Marra, 2017; Bowler, Heldbjerg, Fox,  
111 Jong, & Böhning-Gaese, 2019). Therefore, ecosystem engineering activities may be better  
112 understood by looking at the distribution and abundance of their food resources.

113           Woodpeckers are avian ecosystem engineers that have a large proportion of insects in  
114 their diet (Jones et al., 1994; Tarbill et al., 2015), and control the location, construction, and  
115 availability of nesting cavities, a limiting resource for secondary cavity nesting birds (SCB; i.e.  
116 species that require a cavity to nest in but cannot create the cavity themselves). Woodpeckers are  
117 primary excavators of nesting cavities, often creating multiple cavities within their home range  
118 per year to avoid predation, external parasite buildup, and cavity wood degradation (Loye &  
119 Carroll 1998; Husak & Husak, 2002; Wiebe, 2017). Once abandoned, these cavities are used by  
120 a variety of secondary cavity nesting species (Martin & Eadie, 1999, Pakkala, Tiainen, Piha, &  
121 Kouki, 2019). Woodpeckers select nesting sites based on characteristics that protect their eggs  
122 and nestlings from predation, tending to nest high in moderately to heavily decayed trees with  
123 wide diameters at breast height (DBH), and with limited vegetation covering the cavity entrance  
124 (vegetation cover, Mannan, Meslow, & Wight, 1980; Li & Martin, 1991; Loye & Carroll, 1998;  
125 Newlon, 2005; Jusino et al., 2016). Additionally, the shape of woodpecker cavities functions to  
126 exclude nest predators by having small entrance holes and deep depths (Sedgwick & Knopf,

127 1990; Li and Martin, 1991; Martin, Aitken, & Wiebe, 2004; Rhodes, O'donnell, & Jamieson,  
128 2009). Given the nest construction preferences of woodpeckers, the cavities they leave behind  
129 are often superior nesting spaces when compared to naturally occurring cavities, both of which  
130 are used by SCB (Martin & Li, 1992; Maziarz, Broughton, & Wesolowski, 2017).

131 Woodpecker resources can be defined both in terms of food (mainly wood burrowing  
132 insects, largely in the order Coleoptera) and in the number of trees suitable for excavation  
133 (Bonnot, Millspaugh, & Rumble, 2009; Rota, Rumble, Lehman, Kesler, & Millspaugh, 2015).  
134 These resources have been shown to be directly linked to woodpecker nest site location and  
135 home range sizes (e.g. the area used by a bird in its daily movements) (Worton, 1989; Powell,  
136 2000; Wiktander, Olsson, & Nilsson, 2001; Pasinelli, 2007). For example, the Black-backed  
137 woodpecker (*Picoides arcticus*) selects nesting sites based on infestations of the mountain pine  
138 beetles (*Dendroctonus ponderosae*) (Rota et al., 2015), and the Three-toed woodpecker's  
139 (*Picoides dorsalis*) home range size is negatively correlated with the number of trees with  
140 suitable DBH for cavity excavation (Pechacek & d'Oleire-Oltmanns, 2004). However, no studies  
141 to date have looked at the impact of food resources on both the nest site location and home range  
142 sizes of woodpeckers, which in turn directly impacts neighboring SCB.

143 The Golden-fronted woodpecker (GFWO, *Melanerpes aurifrons*), is a poorly studied,  
144 medium sized bird, whose range extends from Central America to Texas (Wetmore, 1948; Sauer,  
145 Link, Failon, Pardieck, & Ziolkowski, 2013; Schroeder, Boal, & Glasscock, 2013). GFWO  
146 numbers are in decline across their Texas distribution, and are considered a species of concern in  
147 the Texas Wildlife Action Plan (Bender, 2007). As with other woodpecker species, GFWO act as  
148 ecosystem engineers, providing nesting cavities for SCB throughout their range (Husak &  
149 Maxwell, 1998). Determining the factors that influence the nest site location and construction of

150 cavities is crucial to not only understand the conservation needs of GFWO, but also for the  
151 conservation and basic ecology of SCB that may rely on the cavities GFWO create.

152 To investigate relationships between the GFWO and local SCB nesting successes, we  
153 conducted an observational study on GFWO nesting success ( $\geq 1$  fledgling) in relation to nesting  
154 site locations, home range sizes, local insect biomass, and cavity construction, along with the  
155 nesting success of the four most common SCB in our study area, the Black-crested Titmouse  
156 (BCTI; *Baeolophus atricristatus*), Ash-throated Flycatcher (ATFL; *Myiarchus cinerascens*),  
157 Brown-crested Flycatcher (BCFL; *Myiarchus tyrannulus*), and Bewick's Wren (BEWR;  
158 *Thryomanes bewickii*) in the southern Texas Tamaulipan Brushlands (Baumgardt, Morrison,  
159 Brennan, Pierce, & Campbell, 2019).

160 The objectives of our study were to determine 1) the role of insect availability in nest site  
161 location and home range size of GFWO, 2) the role of nest metrics (e.g. DBH, vegetation cover)  
162 in the nesting success of GFWO and the four species of SCB, and 3) if SCB tended to nest more  
163 in abandoned woodpecker cavities and had differing nesting success in abandoned woodpecker  
164 cavities compared to natural cavities. We predicted that 1) insect abundance would be greater at  
165 GFWO occupied sites versus GFWO unoccupied sites and that home range size would be  
166 negatively correlated with the availability of insect orders commonly eaten by birds, 2) the same  
167 cavity metrics would influence nest success in both GFWO and SCB species and 3) that SCB  
168 would tend to nest in, and have higher nest success in abandoned woodpecker cavities compared  
169 to natural cavities, and that abandoned woodpecker cavities would share characteristics making  
170 them more suitable for nesting birds, compared to natural cavities.

171

## 172 2. MATERIALS AND METHODS

### 173 2.1 Study Area

174 Our study was conducted on the East Foundation's ~61,000 ha San Antonio Viejo (SAV) ranch  
175 located in Jim Hogg and Starr counties, ~25 km south of Hebbronville, south Texas. This area is  
176 representative of the Tamaulipan/Mezquital Thornscrub ecological region containing unique  
177 plants and animal communities within brush covered dunes, grasslands punctuated with clusters  
178 of trees, and open woods of mesquite (*Prosopis glandulosa*). Annual rainfall during the study  
179 year (2019) for this region was ~30 cm and the mean temperature during the breeding season  
180 (March - July) was ~27.8° C (PRISM Climate Group 2019), similar to the 30 year norm for this  
181 region (PRISM Climate Group 2019). The SAV supports approximately 70 residential bird  
182 species and 45 migratory species (Baumgardt et al., 2019).

### 183 2.2 Nest Location and Monitoring

184 We used the East Foundation's extensive long-term breeding bird dataset, constructed over 6  
185 years, to create a heat map of areas most likely to contain nesting GFWO (Baumgardt et al.,  
186 2019). We then used the Point Density tool in ArcGIS version 10.3 (Environmental Systems  
187 Research Institute, Redlands, CA, USA) to take a 500 m<sup>2</sup> fishnet sample, and interpolate density  
188 values across our study location. Within areas of high GFWO density, we placed 12 1-km<sup>2</sup>  
189 survey plots (Figure S1) and from mid-April to late May, 2019 we visited each plot four times  
190 using the spot mapping technique to locate nesting GFWO (Martin & Geupel, 1993).

191 After locating GFWO nests, we searched 150 m<sup>2</sup> grids centered around each nest every 3-  
192 5 days between April and July 2019 to document active SCB nests (Rodewald, 2004). To select  
193 GFWO unoccupied sites, we placed 150m<sup>2</sup> grids 300 m away from occupied sites that had the

194 same vegetation association but no observed GFWO activity (sightings, calling, drilling,  
195 foraging, and nesting) and searched for SCB nests in the same way. The vegetation associations  
196 were determined by the East Foundation's hierarchical vegetation classification system, created  
197 in 2011-2012 where a vegetation association was defined by the dominant and subdominant  
198 species (Snelgrove, Dube, Skow & Engeling, 2013). To determine SCB nesting tendencies and  
199 any differences in cavity metrics between abandoned woodpecker cavities and natural cavities,  
200 we recorded and monitored all empty cavities we found in each grid throughout the breeding  
201 season.

202 We monitored each SCB and GFWO nest every 2-5 days to determine nest success; a  
203 nest was considered successful if  $\geq 1$  fledgling was observed outside the nest. After fledging, we  
204 measured the following nest metrics that have historically been predictors of cavity nesting  
205 success: the height of the nest measured from the center of the cavity opening to the base of the  
206 tree (height), the tree's DBH, diameter of the cavity opening (opening), the depth of the cavity  
207 (depth), and decay ranking (decay), where a rank of one indicated a live tree and rank seven  
208 indicated a dead tree with no branches, bark, and soft stem (Dobkin, Pretare, & Pyle, 1995;  
209 Bonar, 2001; Cockle, Martin, & Wesolowski, 2011; Berl. Edwards, & Bolsinger, 2015). Because  
210 increased vegetation cover may be detrimental for cavity nesting birds (Schaaf, 2020), we used  
211 0.5 x 0.5 m<sup>2</sup> cover boards to estimate the percentage of vegetation cover at each cavity (Nudds,  
212 1997; Chotprasertkoon, Pierce, Savini, Round, Sankamethawee, & Gale, 2017).

### 213 **2.3 Insect Sampling and Home range delineation**

214 To determine if GFWO were choosing nesting sites and home range sizes based on available  
215 insects, we compared home range sizes to the available insect biomass within. Home range size  
216 was estimated by constructing minimum convex polygons (MCPs) on a randomly chosen subset

217 of the home ranges ( $n = 24$ ). We constructed MCPs by recording male movements over four, 30-  
218 minute visits that began after observing a male leave their nest ([Dudley & Saab, 2007](#)). We  
219 recorded 120 observation points for each male and built MCPs using the minimum bounding  
220 geometry tool in ArcGIS version 10.3 (Environmental Systems Research Institute, Redlands,  
221 CA, USA)

222         Within the same subset of home ranges, along with the associated unoccupied sites, we  
223 quantified the availability of insects with an array of 11 sweep net sampling locations from the  
224 center of the site (0 m) outwards in 15 m increments to 150 m (see Figure S2), visiting each site  
225 once per week from May to mid-July 2019 ([Doxon, Davis, & Fuhlendorf, 2011](#)). We sorted the  
226 insects by order, dried them using an Elite Eliminator Heater set at 55°C, and weighed them  
227 every 24 hours until their mass stabilized.

## 228 **2.4 Statistical analysis**

### 229 **2.4.1. Insect availability**

230 We averaged insect mass over the seven visits across sampling locations within a home range  
231 and summed all sampling locations per site to get a single measure of insect order biomass per  
232 site. We used Mann-Whitney U t-tests to determine differences ( $P = 0.05$ ) in insect abundance  
233 between sites occupied by GFWO and unoccupied sites, and used Spearman's Rho to test for  
234 significant correlations between each insect order's biomass and each male GFWO's home range  
235 size ([Field et al., 2012](#)).

### 236 **2.4.2. GFWO Nest Success**

237 We created logistic regression models in RStudio version 1.15.2, (R Core Team 2013) with the  
238 package *car* ([Fox & Weisberg, 2019](#)) using recorded cavity metrics to predict GFWO nest

239 success. We considered variance inflation factors (VIFs) >5 as indicators of multicollinearity  
240 between variables and z-scaled all continuous variables to account for varying units of  
241 measurement (O'Brien, 2007). To create candidate models, we used the *MuMIn* package  
242 (Barton, 2020) in R to generate a model selection table (Burnham & Anderson, 2002; Field,  
243 Miles, & Field, 2012), and evaluated model fit using AIC adjusted for small sample sizes (AICc)  
244 (Burnham & Anderson, 2002). Models that had  $\geq 10\%$  of the weight of the top model were  
245 considered candidate models for model averaging (Burnham & Anderson, 2004; Mazerolle,  
246 2006). Using the R package *AICcmodavg* (Mazerolle, 2020) we estimated the parameter  
247 coefficients through model averaging and determined which parameters were significant using  $P$   
248  $\leq 0.05$  and corresponding confidence intervals.

#### 249 **2.4.3 SCB Nest Success**

250 To compare the structure of abandoned woodpecker cavities to natural cavities we used Welch's  
251 tests for each set of measurements taken on all cavities encountered (Field et al., 2012). We then  
252 followed the same steps to create species specific logistic regression and model averages for the  
253 four SCB (Nemes, Jonasson, Genell, & Steineck, 2009; Field et al., 2012). Observations on the  
254 ATFL and the BCFL were combined given the similarity of their body metrics and life history  
255 traits, and hereafter are referred to as ATBC (Cardiff and Dittmann 2000). We used the same six  
256 cavity metrics, with the addition of whether the nest was located in an abandoned woodpecker  
257 cavity or a natural cavity (cavity type). As before, we used the R packages *MuMIn* and  
258 *AICcmodavg* to evaluate candidate models and average parameter coefficients per species.

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260

261 **3. RESULTS**

262 **3.1 Insects define GFWO localities**

263 We collectively spent 560 hours recording GFWO activities and found 55 GFWO nests, along  
264 with an additional 2,880 observation hours to define GFWO home ranges. We spent 220 hours  
265 collecting insect samples across 24 of these home ranges and 24 unoccupied equivalent ranges,  
266 and found that insect orders Coleoptera ( $W = 19$ ,  $P < 0.001$ ), Orthoptera ( $W = 13$ ,  $P < 0.001$ ),  
267 and Hymenoptera ( $W = 186$ ,  $P < 0.036$ ) had significantly higher masses on GFWO occupied  
268 sites than unoccupied sites. All other insect orders were not significantly different.

269 GFWO home range sizes were negatively correlated with the same three orders of  
270 insects, Coleoptera ( $P < 0.001$ ,  $\rho = -0.74$ ,  $n = 24$ ), Orthoptera ( $P = 0.007$ ,  $\rho = -0.55$ ,  $n = 24$ ),  
271 and Hymenoptera ( $P = 0.009$ ,  $\rho = -0.53$ ,  $n = 24$ ) (see Figure 1). The biomass of Phasmatodea  
272 was positively correlated ( $P = 0.045$ ,  $\rho = 0.41$ ,  $n = 24$ ) with GFWO home range size, and all  
273 other insect orders were not significantly correlated.

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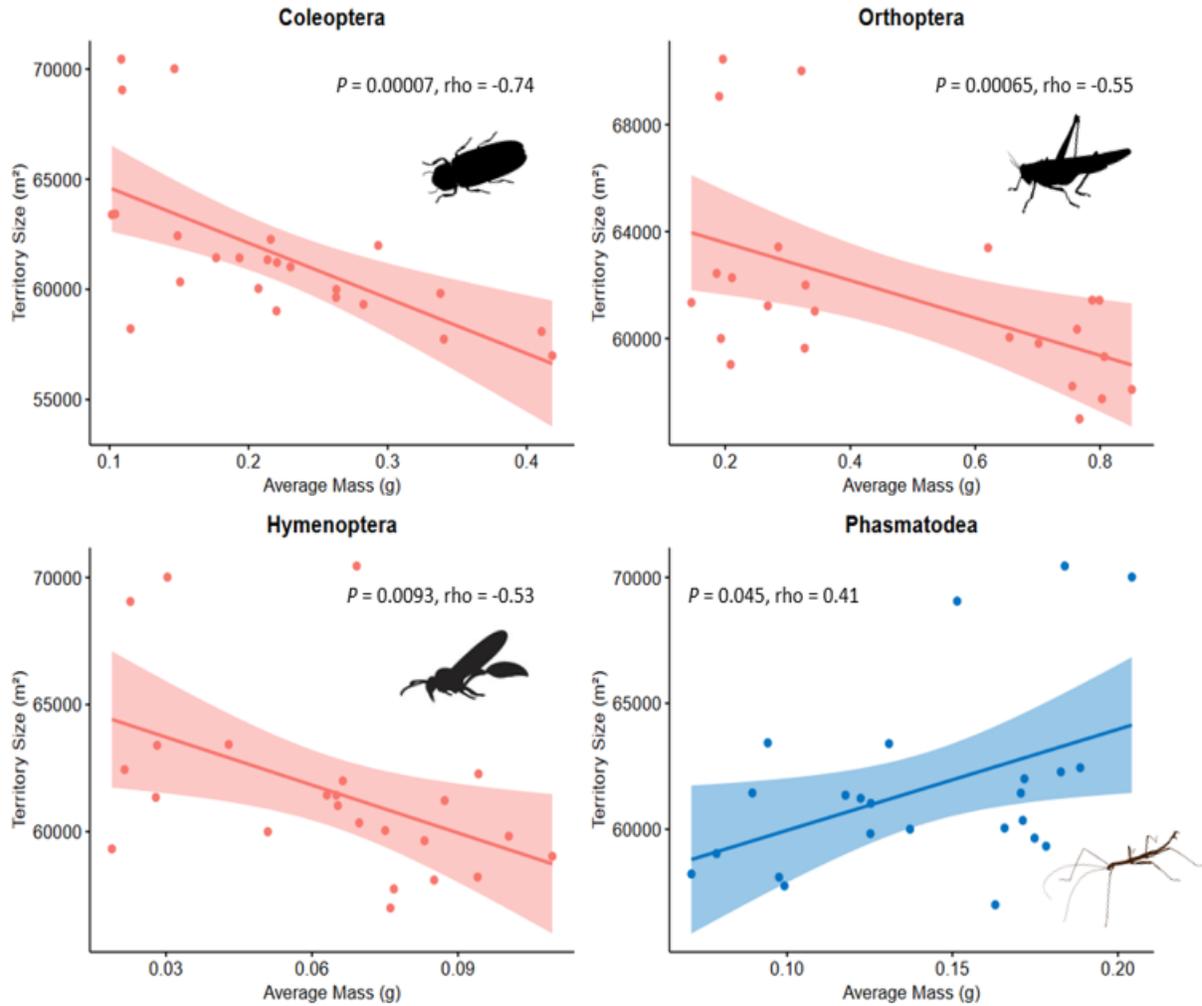
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**Figure 1:** Scatter plots of Golden-fronted woodpecker home range size (m<sup>2</sup>) correlated with average mass (g) of significant insect orders. Shaded areas represent 95% confidence intervals. Data collected with sweep nets on the San Antonio Viejo Ranch, East Foundation in south Texas, during the summer of 2019.

281 **3.2 GFWO nest success**

282 The mean height for a GFWO cavity within our study was 2.3 m ± 0.26, the mean DBH of the  
 283 nesting tree was 52 cm ± 6.2, the mean cavity diameter was 9 cm ± 0.8, the mean depth was 7  
 284 cm ± 0.7, and the mean vegetation cover was 43% ± 6.3. Over 25% of GFWO nests were in trees  
 285 with decay class 1 (Table 1).

286

**Table 1:** Nesting tree decay (1 = live tree, 7 = dead, decayed tree), for each cavity nesting bird found within the study. Count and percent of that species within each decay rank are shown for each species of secondary cavity nesting bird, along with the primary cavity nesting bird, the Golden-fronted woodpecker. The data on the Ash-throated and Brown-crested Flycatchers were combined due to similar life history traits between species. Data was collected on the San Antonio Viejo Ranch, East Foundation in south Texas during the summer of 2019.

Species	Decay						
	1 (%)	2 (%)	3 (%)	4 (%)	5 (%)	6 (%)	7 (%)
Ash-throated/Brown-crested Flycatcher	14 (13.7)	11 (10.8)	16 (15.7)	23 (22.5)	19 (18.6)	16 (15.7)	3 (2.9)
Black-crested Titmouse	7 (17.9)	5 (12.8)	5 (12.8)	3 (7.7)	10 (25.6)	6 (15.4)	3 (7.7)
Bewick's Wren	16 (20.3)	10 (12.7)	13 (16.5)	15 (19)	14 (17.8)	11 (13.9)	0 (0)
Golden-fronted Woodpecker	14 (25.5)	8 (14.5)	7 (12.7)	4 (7.3)	7 (12.7)	9 (16.4)	6 (10.9)

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289 No VIFs were >5, thus all predictors were entered into the global model (see Table S1 for  
 290 candidate model selection). Model averaging suggested that GFWO nests were less likely to be  
 291 successful as decay increased ( $\beta = -0.91$ ), and were more likely to be successful as vegetation  
 292 cover increased ( $\beta = 0.10$ ) (Table 2). Looking at the magnitude of effect, decay was ten times  
 293 stronger at predicting successful nests for GFWO than vegetation cover, though both were  
 294 significant. Notably, with every unit increase in decay (ranked 1-7) nest success for the GFWO  
 295 dropped 0.41.

**Table 2:** Model averaged estimates with 95% confidence intervals (CI) for variables retained in the candidate model sets that predicted cavity nesting bird nesting success. All continuous variables used to create candidate models were z-scaled. Decay was ranked 1 = live tree, 7 = dead, decayed tree. Cavity Type = whether the nest was located in an abandoned woodpecker cavity or a naturally occurring one, DBH = diameter of the nesting tree at breast height. Flycatchers = combined observations of Ash-throated and Brown-crested flycatchers. Data was collected on the San Antonio Viejo Ranch, East Foundation in south Texas during the summer of 2019. Bootstrapping was used to obtain CI. SE is standard error and bolded variables are significant ( $P < 0.05$ )

	Model averaged $\beta$	SE	P	95% CI	
				Lower	Upper
<b>Golden-fronted woodpecker (n = 55)</b>					
<b>Decay</b>	<b>-0.91</b>	<b>0.41</b>	<b>0.015</b>	<b>-1.71</b>	<b>-0.1</b>
<b>Vegetation Cover</b>	<b>0.09</b>	<b>0.05</b>	<b>0.028</b>	<b>-0.001</b>	<b>0.19</b>
DBH	0.12	0.3	0.362	-0.48	0.71
Diameter of Opening	0.05	0.33	0.445	-0.59	0.69
Height	0.02	0.28	0.472	-0.52	0.56
Depth	0.02	0.18	0.46	-0.33	0.37
<b>Bewick's wren (n = 79)</b>					
Decay	-0.03	0.14	0.421	-0.30	0.24
<b>Vegetation Cover</b>	<b>0.06</b>	<b>0.02</b>	<b>0.002</b>	<b>0.02</b>	<b>0.10</b>
DBH	0.63	0.49	0.104	-0.34	1.59
Diameter of Opening	-0.04	0.18	0.408	-0.40	0.31
Height	0.01	0.17	0.480	-0.34	0.33
Depth	< 0.01	0.17	0.500	-0.34	0.34
<b>Cavity Type (natural)</b>	<b>1.92</b>	<b>0.95</b>	<b>0.023</b>	<b>0.05</b>	<b>3.78</b>
<b>Flycatchers (n = 102)</b>					
<b>Decay</b>	<b>-0.40</b>	<b>0.19</b>	<b>0.018</b>	<b>-0.77</b>	<b>-0.03</b>
Vegetation Cover	< 0.01	0.01	0.383	-0.01	0.01
DBH	< 0.01	0.14	0.498	-0.27	0.27
Diameter of Opening	-0.63	0.39	0.056	-1.40	0.14
Height	0.06	0.19	0.385	-0.32	0.43
Depth	-0.05	0.17	0.388	-0.39	0.29
<b>Cavity Type (natural)</b>	<b>3.54</b>	<b>0.77</b>	<b>&lt; 0.001</b>	<b>2.02</b>	<b>5.05</b>
<b>Black-crested titmouse (n = 39)</b>					
<b>Decay</b>	<b>-1.02</b>	<b>0.41</b>	<b>0.008</b>	<b>-1.83</b>	<b>-0.21</b>
Vegetation Cover	0.03	0.03	0.180	-0.03	0.08
DBH	0.07	0.29	0.403	-0.49	0.63
Diameter of Opening	0.02	0.21	0.460	-0.39	0.43
Height	-0.05	0.29	0.429	-0.63	0.52
Depth	< 0.01	0.21	0.497	-0.42	0.42
<b>Cavity Type (natural)</b>	<b>2.53</b>	<b>1.28</b>	<b>0.025</b>	<b>0.03</b>	<b>5.04</b>

*Note:* Candidate models were chosen if they had an AICc weight  $\geq 10\%$  of the AICc weight of the top model.

### 296 3.3 Cavities and SCB nesting success

297 Across all cavities found, whether a nest had been initiated in it or not, abandoned woodpecker  
 298 cavities were significantly different than natural cavities: abandoned woodpecker cavities were  
 299 built 42% higher in less decayed trees with 20% larger DBH than natural cavities and had 18%  
 300 higher vegetation cover (Table 3). The size of the entrance hole and the depth of the cavity were  
 301 not significantly different between nest types.

302

**Table 3:** Results of Welch's t-test comparing differences between abandoned woodpecker cavities (AWC) and natural cavities (NC). DBH = diameter of the nesting tree at breast height, Decay (1 = live tree, 7 = dead, decayed tree). Data was collected on the SAV Ranch, East Foundation during 2019.

	P	t	AWC		NC	
			Average	(±)	Average	(±)
<b>Decay</b>	<b>&lt; 0.001</b>	<b>9.3</b>	<b>3</b>	<b>0.3</b>	<b>4</b>	<b>0.3</b>
<b>Vegetation Cover (%)</b>	<b>&lt; 0.001</b>	<b>6.4</b>	<b>50</b>	<b>1.6</b>	<b>41</b>	<b>1.8</b>
<b>DBH (cm)</b>	<b>&lt; 0.001</b>	<b>8.3</b>	<b>63.1</b>	<b>1.5</b>	<b>50.2</b>	<b>1.2</b>
Opening (cm)	0.321	20.1	13.6	4.2	15.2	6.7
<b>Height (m)</b>	<b>&lt; 0.001</b>	<b>22.1</b>	<b>1.9</b>	<b>0.2</b>	<b>1.1</b>	<b>0.15</b>
Depth (cm)	0.297	9.7	20.2	5.7	18.4	7.3

303

304 Model averaging for the BEWR suggested that cavity type was 15 times stronger at predicting  
 305 successful nests than vegetation cover, though both were significant (Table 2; see Table S1 for  
 306 candidate model selection), with nests more likely to be successful as vegetation cover increased  
 307 ( $\beta = 0.06$ ), and if nests were built in an abandoned woodpecker cavity over a natural cavity ( $\beta =$   
 308 0.95). Model averaging for both the BCTI and the ATBC suggested that decay and the cavity  
 309 type were significant predictors for nest success. As with the GFWO, with every unit increase in  
 310 decay, nest success dropped 0.19 for ATBC and 0.41 for BCTI. Again, cavity type was the  
 311 strongest predictor; cavity type was 3 times stronger at predicting nest success than decay for the

312 BCTI, and was 4 times stronger than decay for the ATBC. Across SCB species, cavity type was  
313 the strongest predictor of nest success.

#### 314 **4. DISCUSSION**

315 Decades of field observations in a range of bird species suggest the importance of insects to birds  
316 during the breeding season, as protein demands are increased while producing eggs and  
317 provisioning nestlings ([Capinera, 2011](#), [Vitz & Rodewald, 2012](#)). We identify correlations  
318 between food resources and GFWO nest site location and home range size, along with nest  
319 cavity characteristics that facilitate successful broods and reveal the importance of abandoned  
320 woodpecker cavities for secondary cavity nesting birds. Additionally, our results suggest a novel  
321 trade-off between excavating live trees versus dead/decaying trees, evident in the differences in  
322 nest success between natural cavities and abandoned woodpecker cavities.

#### 323 **Resource driven site location**

324 All recorded orders of insects collected within our study were found at all occupied and  
325 unoccupied site types, though not every insect order was found at each sweep netting location,  
326 nor at every visit. Previous literature has indicated that Coleoptera and Hymenoptera are in high  
327 proportions of woodpecker diets ([Beckwith & Bull, 1985](#); [Hess & James, 1998](#); [Fayt, Machmer,](#)  
328 [& Steeger, 2005](#); [Pechacek & Kristin, 2010](#)), and as we predicted in our first objective, the  
329 biomass of both of these insect orders were higher around GFWO nests than unoccupied sites  
330 and increases in their biomass corresponded with decreased GFWO home ranges, up to 15,000  
331 m<sup>2</sup>. In addition, we found similar relationships between Orthoptera and GFWO sites and home  
332 ranges.

333 Our findings indicate that resource availability (e.g. insect biomass) may be driving the  
334 location and home range sizes of this ecosystem engineer, as GFWO nests were located in areas  
335 that corresponded with insect availability, and home ranges shrank in correlation with increases  
336 in those same insect orders. This is in accordance with previous literature which indicates that  
337 woodpeckers reduce their defended areas when resources were abundant, and chose nesting sites  
338 based on resource availability (Pasinelli, 2000; Tingley, Wilkerson, Bond, Howell, & Siegel.,  
339 2014). The differences we found in insect biomass between occupied and unoccupied sites were  
340 most likely due to fine scale variation in vegetation and water availability indistinguishable by  
341 our vegetation associations (Huang, Zhao, & von Gadow, 2015).

#### 342 **Interconnected nesting success**

343 In our second and third objectives, we predicted that the same cavity metrics that influenced  
344 GFWO nest success would also influence SCB, and that SCB would have higher nest success in  
345 abandoned woodpecker cavities. As predicted, all SCB had higher nest success rates in  
346 abandoned woodpecker cavities than in natural cavities and cavity type was the strongest  
347 predictor for all species, with the BEWR having the least impact, followed by the BCTI, and  
348 largest influence on ATBC. Additionally, GFWO had higher success in trees with lower decay  
349 and higher vegetation cover, which was mirrored in SCB; BCTI and ATBC were more likely to  
350 produce fledglings in trees with low decay, and BEWR were more likely to produce fledglings in  
351 cavities with high vegetation cover. The BEWR was the only species not impacted by decay,  
352 potentially explained by its generalistic nesting behavior ([Taylor, 2003](#)). We observed successful  
353 BEWR nests built in metal pipes or direct sun, thus experiencing wide temperature swings  
354 throughout the day, indicating that unstable nesting environments may be a deterrent for other  
355 cavity nesting birds, but not this species.

356           Also in line with our third objective, we predicted that abandoned woodpecker cavities  
357 would share characteristics making them better nesting cavities than natural ones. To this, SCB  
358 within our study had higher success rates within abandoned woodpecker cavities (81-93%), than  
359 in natural cavities (41-56%). The structure of abandoned woodpecker cavities present on our  
360 sites were distinctly different from their natural counterparts; on average they were significantly  
361 higher in trees, of lower decay, smaller DBH, and increased vegetation cover, all characteristics  
362 that protect eggs and fledglings from shifting internal temperatures and predation (Copeyon,  
363 1990; Ojeda, Suarez, & Kitzberger, 2007; Pakkala et al., 2019). Considering that SCB are reliant  
364 on pre-existing cavities to create their nests, the factors that drive the creation and design of  
365 woodpecker cavities may then dictate the success of local SCB.

### 366 **Tree decay and vegetation cover: a possible role for temperature**

367 We found a higher than expected number of GFWO nests within live trees. Previous literature on  
368 woodpecker nesting ecology has indicated a preference for excavating cavities in partially to  
369 fully decayed trees, which require less energy and time than dense, live wood (Conner, Miller, &  
370 Adkisson, 1976; Cockle et al., 2011; Blanc & Martin, 2012). However, these studies have  
371 focused on temperate regions such as northwestern, northeastern United States, Canada, and  
372 European countries where breeding season temperature rarely exceeds 35° C and occasionally  
373 reach freezing during the early spring (Conner et al., 1976; Blanc & Martin, 2012; Seavy,  
374 Burnett, & Taille, 2012). In contrast, the mean breeding season temperature at our study site in  
375 southern Texas was 27.8° C and daytime temperatures frequently reached over 42.2° C  
376 Currently, there is little information on how cavity nesting birds regulate nest temperature,  
377 though some species may modulate incubation initiation and duration in relation to temperature  
378 (Coe, Beck, Chin, Jachowski, & Hopkins, 2015; Simmonds, Sheldon, Coulson, & Cole, 2017)

379 and there are reports of GFWO clinging to the sides of the cavity which could be an attempt to  
380 reduce heat transfer (Skutch, 1969). Nest temperature is also affected by nest site location and  
381 cavity design (although not always) (Butler, Whitman & Dufty, 2009; Zingg, Arlettaz & Schaub,  
382 2010; Sonnenberg, Branch, Benedict, Pitera & Pravosudov, 2020).

383 Tree decay, in particular, affects thermoregulation of the nest cavity, in that live trees -  
384 with higher water content- provide greater insulation against high and low temperature extremes  
385 (Grüebler, Widmer, Korner-Nievergelt & Naef- Daenzer, 2014). However, the same trait that  
386 makes live trees good insulators also makes them more costly to excavate; on average, live trees  
387 are denser than partially dead or decaying trees. Therefore, these birds may be facing an  
388 energetic trade-off; whether to put additional effort into excavating a dense live tree- which has  
389 higher water content and is better able to thermoregulate eggs and nestlings- or save time and  
390 energy by excavating a less stable decayed tree and risk eggs and nestlings overheating.

391 This possible role for temperature in nest site selection and structure is further  
392 strengthened by the trend we observed in vegetation cover, with cavity nesters like the GFWO  
393 and the BEWR having higher success in cavities with increased vegetation cover. While the  
394 effect size for vegetation ( $\beta$  ranged from 0.02 to 0.05) seems small at first, across the large range  
395 of possibilities for cover (1-100) this variable showed a strong effect. For example, with a 15  
396 percent increase in vegetation cover, the effect size for the BEWR grew to 0.30 and the same  
397 increase in vegetation cover for the GFWO resulted in an effect size of 0.75, rivaling that of  
398 stronger predictors such as decay and cavity cover. Again, these results contrast with previous  
399 literature on cavity nesters which indicated a preference for exposed cavities due to increased  
400 visibility of approaching predators (Mannan et al., 1980; Li & Martin, 1991; Loye & Carroll,  
401 1998; Newlon, 2005; Jusino et al., 2016). Vegetated cavities in this region may provide increased

402 shade and thus reduced internal temperatures, resulting in another tradeoff, one between  
403 temperature regulation and predation.

#### 404 **Conclusion**

405 Here we evaluated the link between food resources and an ecosystem engineer, and the  
406 subsequent influence of this engineer on local secondary cavity nesters. We observed that  
407 GFWO nest site location and home range size was positively correlated to biomass of the same  
408 three orders of insects that make up large proportions of their diet, and that all SCB had higher  
409 nest success in abandoned woodpecker cavities than natural cavities. Thus, GFWO nest in areas  
410 with abundant food and SCB reap the benefits of the stable cavities they leave behind, along with  
411 opportunistically high insect loads. Our results also suggest that GFWO nest characteristics may  
412 influence nest success in ways that differ from more temperate species, indicating future research  
413 avenues into energetics and predation pressure tradeoffs in high temperature regions.  
414 Additionally, management for woodpeckers and SCB in southern Texas should not focus on the  
415 availability of snags (a common management strategy for woodpeckers in temperate climates),  
416 but on the number of live trees with a DBH wide enough for nesting.

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## 423 **References**

- 424 Bangert, R. K., & Slobodchikoff, C. N. (2004). Prairie dog engineering indirectly affects beetle  
425 movement behavior. *Journal of Arid Environments*, 56(1), 83-94. [doi.org/10.1016/S0140-](https://doi.org/10.1016/S0140-1963(02)00322-1)  
426 [1963\(02\)00322-1](https://doi.org/10.1016/S0140-1963(02)00322-1)  
427
- 428 Barton, K. (2020) Package ‘MuMIn’ in R, Version 1.43.17.  
429 <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>  
430
- 431 Baumgardt, J. A., Morrison, M. L., Brennan, L. A., Pierce, B. L., & Campbell, T. A. (2019).  
432 Development of Multispecies, Long-Term Monitoring Programs for Resource Management.  
433 *Rangeland Ecology & Management*, 72(1), 168-181. [doi.org/10.1016/j.rama.2018.07.010](https://doi.org/10.1016/j.rama.2018.07.010)  
434
- 435 Beckwith, R. C., & Bull, E. L. (1985). Scat analysis of the arthropod component of pileated  
436 woodpecker diet. *The Murrelet*, 66(3), 90-92. [Doi: 10.2307/3535167](https://doi.org/10.2307/3535167)  
437
- 438 Bender, S. (2007). Planning for wildlife in the lone star state. *Endangered Species Update*, 24(1),  
439 S42-S42.  
440
- 441 Benton, T. G., Bryant, D. M., Cole, L., & Crick, H. Q. (2002). Linking agricultural practice to  
442 insect and bird populations: a historical study over three decades. *Journal of applied ecology*,  
443 39(4), 673-687. [doi.org/10.1046/j.1365-2664.2002.00745.x](https://doi.org/10.1046/j.1365-2664.2002.00745.x)  
444
- 445 Berl, J. L., Edwards, J. W., & Bolsinger, J. S. (2015). Scale-dependent and multi-metric nest  
446 habitat thresholds for Red-headed Woodpeckers at the northern periphery of their range. *The*  
447 *Condor: Ornithological Applications*, 117(2), 203-216. [doi.org/10.1650/CONDOR-14-133.1](https://doi.org/10.1650/CONDOR-14-133.1)  
448
- 449 Blanc, L. A., & Martin, K. (2012). Identifying suitable woodpecker nest trees using decay  
450 selection profiles in trembling aspen (*Populus tremuloides*). *Forest Ecology and Management*,  
451 286, 192-202. [doi.org/10.1016/j.foreco.2012.08.021](https://doi.org/10.1016/j.foreco.2012.08.021)  
452
- 453 Bonar, R. L. (2001). Pileated Woodpecker habitat ecology in the Alberta foothills (Doctoral  
454 dissertation, University of Alberta).  
455
- 456 Bonnot, T. W., Millspaugh, J. J., & Rumble, M. A. (2009). Multi-scale nest-site selection by  
457 black-backed woodpeckers in outbreaks of mountain pine beetles. *Forest Ecology and*  
458 *Management*, 259(2), 220-228. [doi.org/10.1016/j.foreco.2009.10.021](https://doi.org/10.1016/j.foreco.2009.10.021)  
459
- 460 Bowler, D. E., Heldbjerg, H., Fox, A. D., de Jong, M., & Böhning-Gaese, K. (2019). Long-term  
461 declines of European insectivorous bird populations and potential causes. *Conservation Biology*,  
462 33(5), 1120-1130. [doi.org/10.1111/cobi.13307](https://doi.org/10.1111/cobi.13307)  
463
- 464 Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC  
465 in model selection. *Sociological methods & research*, 33(2), 261-304.

466 [doi.org/10.1177/0049124104268644](https://doi.org/10.1177/0049124104268644)

467

468 Buse, J., Ranius, T., & Assmann, T. (2008). An endangered longhorn beetle associated with old  
469 oaks and its possible role as an ecosystem engineer. *Conservation Biology*, 22(2), 329-337.

470 [doi.org/10.1111/j.1523-1739.2007.00880.x](https://doi.org/10.1111/j.1523-1739.2007.00880.x)

471

472 Butler, M.W., Whitman, B.A. and Dufty, A.M., (2009). Nest box temperature and hatching  
473 success of American kestrels varies with nest box orientation. *The Wilson Journal of*

474 *Ornithology*, 121(4), 778-782. [doi.org/10.1676/08-124.1](https://doi.org/10.1676/08-124.1)

475

476 Cardiff, S.W. and Dittmann, D.L. (2000). Brown-crested flycatcher (*Myiarchus tyrannulus*). *The*  
477 *Birds of North America*, (496), 1-28.

478

479 Conner, R. N., Miller Jr, O. K., & Adkisson, C. S. (1976). Woodpecker dependence on trees  
480 infected by fungal heart rots. *The Wilson Bulletin*, 575-581.

481

482 Copetón crestipardo (*Myiarchus tyrannulus*). *The Birds of North America*, (496), 1-28.

483

484 Copeyon, C. K. (1990). A technique for constructing cavities for the red-cockaded woodpecker.  
485 *Wildlife Society Bulletin (1973-2006)*, 18(3), 303-311.

486

487 Chotprasertkoon, T., Pierce, A. J., Savini, T., Round, P. D., Sankamethawee, W., & Gale, G. A.  
488 (2017). Influence of vegetation cover on nest cavity selection and nesting success of White-

489 rumped Shamas (*Copsychus malabaricus*): An experimental test. *The Wilson Journal of*  
490 *Ornithology*, 129(4), 727-741. [doi.org/10.1676/16-134.1](https://doi.org/10.1676/16-134.1)

491

492 Cockle, K. L., Martin, K., & Wesolowski, T. (2011). Woodpeckers, decay, and the future of  
493 cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and the Environment*,

494 9(7), 377-382. [doi.org/10.1890/110013](https://doi.org/10.1890/110013)

495

496 Coe, B.H., Beck, M.L., Chin, S.Y., Jachowski, C.M. and Hopkins, W.A. (2015). Local variation  
497 in weather conditions influences incubation behavior and temperature in a passerine bird. *Journal*

498 *of Avian Biology*, 46(4), 385-394. [doi.org/10.1111/jav.00581](https://doi.org/10.1111/jav.00581)

499

500

501 Dudley, J. G., & Saab, V. A. (2007). Home range size of black-backed woodpeckers in burned  
502 forests of southwestern Idaho. *Western north american naturalist*, 67(4), 593-600.

503 [doi.org/10.3398/1527-0904\(2007\)67\[593:HRSOBW\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2007)67[593:HRSOBW]2.0.CO;2)

504 Dobkin, D. S., Rich, A. C., Pretare, J. A., & Pyle, W. H. (1995). Nest-site relationships among  
505 cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great

506 Basin. *The Condor*, 97(3), 694-707. [doi.org/10.2307/1369178](https://doi.org/10.2307/1369178)

507

508 Doxon, E. D., Davis, C. A., & Fuhlendorf, S. D. (2011). Comparison of two methods for

- 509 sampling invertebrates: vacuum and sweep-net sampling. *Journal of Field Ornithology*, 82(1),  
510 60-67. [doi.org/10.1111/j.1557-9263.2010.00308.x](https://doi.org/10.1111/j.1557-9263.2010.00308.x)  
511
- 512 Fayt, Philippe, Marlene M. Machmer, and Christoph Steeger. "Regulation of spruce bark beetles  
513 by woodpeckers—a literature review." *Forest Ecology and Management* 206, no. 1-3 (2005): 1-  
514 14. [doi.org/10.1016/j.foreco.2004.10.054](https://doi.org/10.1016/j.foreco.2004.10.054)  
515
- 516 Gruebler, M.U., Widmer, S., Korner-Nievergelt, F. and Naef-Daenzer, B. (2014). Temperature  
517 characteristics of winter roost-sites for birds and mammals: tree cavities and anthropogenic  
518 alternatives. *International Journal of Biometeorology*, 58(5), 629-637.  
519  
520  
521
- 522 Huang, Y., Zhao, Y., Li, S., & von Gadow, K. (2015). The effects of habitat area, vegetation  
523 structure and insect richness on breeding bird populations in Beijing urban parks. *Urban Forestry  
524 & Urban Greening*, 14(4), 1027-1039. [doi.org/10.1016/j.ufug.2015.09.010](https://doi.org/10.1016/j.ufug.2015.09.010)  
525
- 526 Husak, M. S., & Maxwell, T. C. (1998). Golden-fronted woodpecker (*Melanerpes aurifrons*).  
527 *Texas Journal of Science*, 52(4), 275-284.
- 528 Hess, C. A., & James, F. C. (1998). Diet of the red-cockaded woodpecker in the Apalachicola  
529 National Forest. *The Journal of wildlife management*, 509-517. [doi 10.2307/3802324](https://doi.org/10.2307/3802324)  
530
- 531 Husak, M. S., & Husak, J. F. (2002). Low frequency of site fidelity by golden-fronted  
532 woodpeckers. *The Southwestern Naturalist*, 47(1), 110-114. [doi: 10.2307/3672810](https://doi.org/10.2307/3672810)  
533
- 534 Jusino, M. A., Lindner, D. L., Banik, M. T., & Walters, J. R. (2015). Heart rot hotel: fungal  
535 communities in red-cockaded woodpecker excavations. *Fungal Ecology*, 14, 33-43.  
536 [doi.org/10.1016/j.funeco.2014.11.002](https://doi.org/10.1016/j.funeco.2014.11.002)  
537
- 538 Karr, J. R. (1976). Seasonality, resource availability, and community diversity in tropical bird  
539 communities. *The American Naturalist*, 110(976), 973-994. [doi: 10.1086/283121](https://doi.org/10.1086/283121)  
540
- 541 Lill, J. T., & Marquis, R. J. (2003). Ecosystem engineering by caterpillars increases insect  
542 herbivore diversity on white oak. *Ecology*, 84(3), 682-690. [doi.org/10.1890/0012-  
543 9658\(2003\)084\[0682:EEBCII\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0682:EEBCII]2.0.CO;2)  
544
- 545 Li, P., & Martin, T. E. (1991). Nest-site selection and nesting success of cavity-nesting birds in  
546 high elevation forest drainages. *The Auk*, 108(2), 405-418. [doi.org/10.1093/auk/108.2.405](https://doi.org/10.1093/auk/108.2.405)  
547
- 548 Lister, B. C., & Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a  
549 rainforest food web. *Proceedings of the National Academy of Sciences*, 115(44), E10397-  
550 E10406. [doi.org/10.1073/pnas.1722477115](https://doi.org/10.1073/pnas.1722477115)  
551

- 552 Loye, J. E., & Carroll, S. P. (1998). Ectoparasite behavior and its effects on avian nest site  
553 selection. *Annals of the Entomological Society of America*, 91(2), 159-163.  
554 [doi.org/10.1093/aesa/91.2.159](https://doi.org/10.1093/aesa/91.2.159)  
555
- 556 Mannan, R. W., Meslow, E. C., & Wight, H. M. (1980). Use of snags by birds in Douglas-fir  
557 forests, western Oregon. *The Journal of Wildlife Management*, 787-797. [doi: 10.2307/3808306](https://doi.org/10.2307/3808306)  
558
- 559 Martin, K., & Eadie, J. M. (1999). Nest webs: a community-wide approach to the management  
560 and conservation of cavity-nesting forest birds. *Forest Ecology and Management*, 115(2-3), 243-  
561 257. [doi.org/10.1016/S0378-1127\(98\)00403-4](https://doi.org/10.1016/S0378-1127(98)00403-4)  
562
- 563 Martin, K., Aitken, K. E., & Wiebe, K. L. (2004). Nest sites and nest webs for cavity-nesting  
564 communities in interior British Columbia, Canada: nest characteristics and niche partitioning.  
565 *The condor*, 106(1), 5-19. [doi.org/10.1093/condor/106.1.5](https://doi.org/10.1093/condor/106.1.5)  
566
- 567 Martin, Thomas E., and Pingjun Li. "Life history traits of open-vs. cavity-nesting birds."  
568 *Ecology* 73.2 (1992): 579-592. [doi.org/10.2307/1940764](https://doi.org/10.2307/1940764)  
569
- 570 Martin, T. E., & Geupel, G. R. (1993). Nest-Monitoring Plots: Methods for Locating Nests and  
571 Monitoring Success (Métodos para localizar nidos y monitorear el éxito de estos). *Journal of*  
572 *field Ornithology*, 507-519.  
573
- 574 Mazerolle, M. (2006). Improving data analysis in herpetology: using Akaike's Information  
575 Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia*, 27(2), 169-  
576 180. DOI: <https://doi.org/10.1163/156853806777239v922>
- 577 Mazerolle, M. (2020). Package ‘AICcmodavg’ in R. Version 2.3-1.  
578 <https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf>  
579
- 580 Maziarz, M., Broughton, R. K., & Wesolowski, T. (2017). Microclimate in tree cavities and nest-  
581 boxes: implications for hole-nesting birds. *Forest Ecology and Management*, 389, 306-313.  
582 [doi.org/10.1016/j.foreco.2017.01.001](https://doi.org/10.1016/j.foreco.2017.01.001)  
583
- 584 Mikusiński, G. (2006). Woodpeckers: distribution, conservation, and research in a global  
585 perspective. *Annales Zoologici Fennici* 43(2), 86-95. <https://www.jstor.org/stable/23735921>  
586
- 587 Møller, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in  
588 Denmark over 22 years. *Ecology and Evolution*, 9(11), 6581-6587. [doi.org/10.1002/ece3.5236](https://doi.org/10.1002/ece3.5236)  
589
- 590 Narango, D. L., Tallamy, D. W., & Marra, P. P. (2017). Native plants improve breeding and  
591 foraging habitat for an insectivorous bird. *Biological Conservation*, 213, 42-50.  
592 [doi.org/10.1016/j.biocon.2017.06.029](https://doi.org/10.1016/j.biocon.2017.06.029)  
593
- 594 Nemes, S., Jonasson, J. M., Genell, A., & Steineck, G. (2009). Bias in odds ratios by logistic  
595 regression modelling and sample size. *BMC medical research methodology*, 9(1), 56. [Doi:](https://doi.org/10.1186/1471-2288-9-56)

596 [10.1186/1471-2288-9-56](https://doi.org/10.1186/1471-2288-9-56)

597

598 Newlon, K. R. (2005). Demography of Lewis's woodpecker, breeding bird densities, and riparian  
599 aspen integrity in a grazed landscape. MS Thesis. Montana State University, Bozeman. 101 p.

600

601 Nilsson, S. G., Johnsson, K., & Tjernberg, M. (1991). Is avoidance by black woodpeckers of old  
602 nest holes due to predators? *Animal Behaviour*, 41(3), 439-441. [doi.org/10.1016/S0003-  
603 3472\(05\)80845-0](https://doi.org/10.1016/S0003-3472(05)80845-0)

604

605 Nudds, T. D. (1977). Quantifying the vegetative structure of wildlife cover. *Wildlife Society  
606 Bulletin*, 113-117. [Link](#)

607

608 O'Brien, R.M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality  
609 & quantity*, 41(5), 673-690.

610

611 Ojeda, V. S., Suarez, M. L., & Kitzberger, T. (2007). Crown dieback events as key processes  
612 creating cavity habitat for magellanic woodpeckers. *Austral Ecology*, 32(4), 436-445.  
613 [doi.org/10.1111/j.1442-9993.2007.01705.x](https://doi.org/10.1111/j.1442-9993.2007.01705.x)

614

615 Pakkala, T., Tiainen, J., Piha, M., & Kouki, J. (2019). Hole life: survival patterns and reuse of  
616 cavities made by the Lesser Spotted Woodpecker *Dendrocopos minor*. *Ardea*, 107(2), 173-181.  
617 [doi.org/10.5253/arde.v107i2.a4](https://doi.org/10.5253/arde.v107i2.a4)

618

619 Pasinelli, G. (2000). Oaks (*Quercus* sp.) and only oaks? Relations between habitat structure and  
620 home range size of the middle spotted woodpecker (*Dendrocopos medius*). *Biological  
621 Conservation*, 93(2), 227-235. [doi.org/10.1016/S0006-3207\(99\)00137-8](https://doi.org/10.1016/S0006-3207(99)00137-8)

622

623 Pechacek, P., & d'Oleire-Oltmanns, W. (2004). Habitat use of the three-toed woodpecker in  
624 central Europe during the breeding period. *Biological Conservation*, 116(3), 333-341.  
625 [doi.org/10.1016/S0006-3207\(03\)00203-9](https://doi.org/10.1016/S0006-3207(03)00203-9)

626

627 Pechacek, P., & Kristin, A. (2004). Comparative diets of adult and young three-toed  
628 woodpeckers in a European alpine forest community. *The Journal of wildlife management*,  
629 68(3), 683-693. [doi.org/10.2193/0022-541X\(2004\)068\[0683:CDOAAY\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0683:CDOAAY]2.0.CO;2)

630

631 PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 31 Jul  
632 2020.

633

634 R Core Team (2013). R: A language and environment for statistical computing. R Foundation for  
635 Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

636

637 Rhodes, B., O'donnell, C., & Jamieson, I. (2009). Microclimate of natural cavity nests and its  
638 implications for a threatened secondary-cavity-nesting passerine of New Zealand, the South  
639 Island Saddleback. *The Condor*, 111(3), 462-469. [doi.org/10.1525/cond.2009.080030](https://doi.org/10.1525/cond.2009.080030)

640

- 641 Rioux Paquette, S., Pelletier, F., Garant, D., & Bélisle, M. (2014). Severe recent decrease of  
642 adult body mass in a declining insectivorous bird population. *Proceedings of the Royal Society*  
643 *B: Biological Sciences*, 281(1786), 20140649. [doi.org/10.1098/rspb.2014.0649](https://doi.org/10.1098/rspb.2014.0649)
- 644  
645 Robles, H., & Martin, K. (2013). Resource quantity and quality determine the inter-specific  
646 associations between ecosystem engineers and resource users in a cavity-nest web. *PLoS One*,  
647 8(9), e74694. [doi.org/10.1371/journal.pone.0074694](https://doi.org/10.1371/journal.pone.0074694)
- 648  
649 Rodewald, A. D. (2004). Nest-searching cues and studies of nest-site selection and nesting  
650 success. *Journal of Field Ornithology*, 75(1), 31-39. [doi.org/10.1648/0273-8570-75.1.31](https://doi.org/10.1648/0273-8570-75.1.31)
- 651  
652 Rota, C. T., Rumble, M. A., Lehman, C. P., Kesler, D. C., & Millsbaugh, J. J. (2015). Apparent  
653 foraging success reflects habitat quality in an irruptive species, the Black-backed Woodpecker.  
654 *The Condor: Ornithological Applications*, 117(2), 178-191. [doi.org/10.1650/CONDOR-14-112.1](https://doi.org/10.1650/CONDOR-14-112.1)
- 655  
656 Sauer, J. R., Link, W. A., Fallon, J. E., Pardieck, K. L., & Ziolkowski Jr, D. J. (2013). The North  
657 American breeding bird survey 1966–2011: summary analysis and species accounts. *North*  
658 *American Fauna*, 79(79), 1-32. [doi.org/10.3996/nafa.79.0001](https://doi.org/10.3996/nafa.79.0001)
- 659  
660 Schaaf, A. A. (2020). Effects of sun exposure and vegetation cover on woodpecker nest  
661 orientation in subtropical forests of South America. *Journal of Ethology*, 38(1), 117-120. [doi:](https://doi.org/10.1007/s10164-019-00617-2)  
662 [10.1007/s10164-019-00617-2](https://doi.org/10.1007/s10164-019-00617-2)
- 663  
664 Schroeder, E. L., Boal, C. W., & Glasscock, S. N. (2013). Nestling diets and provisioning rates  
665 of sympatric golden-fronted and ladder-backed woodpeckers. *The Wilson Journal of*  
666 *Ornithology*, 125(1), 188-192. [doi.org/10.1676/12-041.1](https://doi.org/10.1676/12-041.1)
- 667  
668 Seavy, N. E., Burnett, R. D., & Taille, P. J. (2012). Black-backed woodpecker nest-tree  
669 preference in burned forests of the Sierra Nevada, California. *Wildlife Society Bulletin*, 36(4),  
670 722-728. [doi.org/10.1002/wsb.210](https://doi.org/10.1002/wsb.210)
- 671  
672 Sedgwick, J. A., & Knopf, F. L. (1990). Habitat relationships and nest site characteristics of  
673 cavity-nesting birds in cottonwood floodplains. *The Journal of wildlife management*, 112-124.  
674 [doi: 10.2307/3808910](https://doi.org/10.2307/3808910)
- 675  
676 Showalter, C. R., & Whitmore, R. C. (2002). The effect of gypsy moth defoliation on cavity-  
677 nesting bird communities. *Forest Science*, 48(2), 273-281.  
678 [doi.org/10.1093/forestscience/48.2.273](https://doi.org/10.1093/forestscience/48.2.273)
- 679  
680 Simmonds, E.G., Sheldon, B.C., Coulson, T. and Cole, E.F. (2017). Incubation behavior  
681 adjustments, driven by ambient temperature variation, improve synchrony between hatch dates  
682 and caterpillar peak in a wild bird population. *Ecology and Evolution*, 7(22), 9415-9425.  
683 [doi.org/10.1002/ece3.3446](https://doi.org/10.1002/ece3.3446)
- 684

- 685 Skutch, A. F. (1969). Life Histories of Central American Birds. Pacific Coast Avifauna No. 31.  
686 Berkeley: Cooper Ornithological Society.  
687
- 688 Snelgrove, A., Dube, A., Skow, K., Engeling, A. (2013) East Wildlife Foundation Atlas. Texas  
689 A&M Institute of Renewable Natural Resources, College Station  
690
- 691 Sonnenberg, B.R., Branch, C.L., Benedict, L.M., Pitera, A.M. and Pravosudov, V.V. (2020).  
692 Nest construction, ambient temperature and reproductive success in a cavity-nesting bird.  
693 *Animal Behaviour*, 165, 43-58. [doi.org/10.1016/j.anbehav.2020.04.011](https://doi.org/10.1016/j.anbehav.2020.04.011)  
694
- 695 Tarbill, G. L., Manley, P. N., & White, A. M. (2015). Drill, baby, drill: the influence of  
696 woodpeckers on post-fire vertebrate communities through cavity excavation. *Journal of Zoology*,  
697 296(2), 95-103. [doi.org/10.1111/jzo.12220](https://doi.org/10.1111/jzo.12220)  
698
- 699 Taylor, R. V. (2003). Factors influencing expansion of the breeding distribution of Bewick's  
700 Wren into riparian forests of the Rio Grande in central New Mexico. *The Southwestern*  
701 *Naturalist*, 48(3), 373-382. [doi.org/10.1894/0038-4909\(2003\)048<0373:FIEOTB>2.0.CO;2](https://doi.org/10.1894/0038-4909(2003)048<0373:FIEOTB>2.0.CO;2)  
702
- 703 Tingley, M. W., Wilkerson, R. L., Bond, M. L., Howell, C. A., & Siegel, R. B. (2014). Variation  
704 in home-range size of Black-backed Woodpeckers. *The Condor: Ornithological Applications*,  
705 116(3), 325-340. [doi.org/10.1650/CONDOR-13-140.1](https://doi.org/10.1650/CONDOR-13-140.1)  
706
- 707 Vitz, A. C., & Rodewald, A. D. (2012). Using stable isotopes to investigate the dietary trophic  
708 level of fledgling songbirds. *Journal of Field Ornithology*, 83(1), 73-84. [doi.org/10.1111/j.1557-](https://doi.org/10.1111/j.1557-9263.2011.00357.x)  
709 [9263.2011.00357.x](https://doi.org/10.1111/j.1557-9263.2011.00357.x)  
710
- 711 Weldon, D. (1986). Exceptional physical properties of Texas mesquite wood. *Forest ecology and*  
712 *management*, 16(1-4), 149-153. [doi.org/10.1016/0378-1127\(86\)90015-0](https://doi.org/10.1016/0378-1127(86)90015-0)  
713
- 714 Wetmore, A. (1948). The golden-fronted woodpeckers of Texas and northern México. *Wilson*  
715 *Bulletin*, 60, 185-186.  
716
- 717 Wiebe, K. L. (2017). Northern flickers only work when they have to: how individual traits,  
718 population size and landscape disturbances affect excavation rates of an ecosystem engineer.  
719 *Journal of Avian Biology*, 48(3), 431-438. [doi.org/10.1111/jav.01180](https://doi.org/10.1111/jav.01180)  
720
- 721 Wiktander, U., Olsson, O., & Nilsson, S. G. (2001). Seasonal variation in home-range size, and  
722 habitat area requirement of the lesser spotted woodpecker (*Dendrocopos minor*) in southern  
723 Sweden. *Biological conservation*, 100(3), 387-395. [doi.org/10.1016/S0006-3207\(01\)00045-3](https://doi.org/10.1016/S0006-3207(01)00045-3)  
724
- 725 Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range  
726 studies. *Ecology*, 70(1), 164-168. [doi.org/10.2307/1938423](https://doi.org/10.2307/1938423)  
727

728 Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases  
729 species richness at the landscape scale. *Oecologia*, 132(1), 96-101. [doi.org/10.1007/s00442-002-](https://doi.org/10.1007/s00442-002-0929-1)  
730 [0929-1](https://doi.org/10.1007/s00442-002-0929-1)

731 Zingg, S., Arlettaz, R. and Schaub, M. (2010). Nestbox design influences territory occupancy  
732 and reproduction in a declining, secondary cavity-breeding bird. *Ardea*, 98(1), 67-75.  
733 [doi.org/10.5253/078.098.0109](https://doi.org/10.5253/078.098.0109)

734

735

736

737

738

739

#### 740 **Books**

741

742 Capinera, J. (2011). *Insects and wildlife: arthropods and their relationships with wild vertebrate*  
743 *animals*. John Wiley & Sons.

744 Field, A., Miles, J., & Field, Z. (2012). *Discovering statistics using R*. Sage Publications

745 Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage,  
746 Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

747

748 Garmendia, A., Cárcamo, S., & Schwendtner, O. (2006). Forest management considerations for  
749 conservation of black woodpecker *Dryocopus martius* and white-backed woodpecker  
750 *Dendrocopos leucotos* populations in Quinto Real (Spanish Western Pyrenees). In *Forest*  
751 *Diversity and Management* (pp. 339-355). Springer, Dordrecht.

752

753 Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. In  
754 *Ecosystem management* (pp. 130-147). Springer, New York, NY.

755

756 Pasinelli, G. (2007). Nest site selection in middle and great spotted woodpeckers *Dendrocopos*  
757 *medius* & *D. major*: implications for forest management and conservation. In *Vertebrate*  
758 *Conservation and Biodiversity* (pp. 457-472). Springer, Dordrecht.

759

760 Powell, R. A. (2000). Animal home ranges and territories and home range estimators. *Research*  
761 *techniques in animal ecology: controversies and consequences* (pp. 65-110). Columbia  
762 University Press, NY.

763

764