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Impacts of the invasive European Starling on two neotropical woodpecker species: agonistic responses and reproductive interactions

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Abstract

The European Starling (*Sturnus vulgaris*) -hereafter 'starling'- has been introduced in many countries, and its South American population recently started expanding exponentially. This invasive species has a worldwide negative impact on the breeding performance of woodpeckers, competing for cavity use. Nevertheless, information is still lacking regarding southern temperate neotropical woodpeckers nest defence strategies and starling effects on woodpeckers' breeding performance. We monitored Campo Flicker (*Colaptes campestris*) and Green-barred Woodpecker (*Colaptes melanochloros*) nests in a native southern temperate forest of central-eastern Argentina, to detect interactions with starlings and to assess the effect of starlings presence on woodpeckers' breeding performance. We assessed whether woodpeckers perform defence behaviours against the starlings by exposing taxidermied starling models to woodpecker breeding pairs. We detected interactions with starlings at 11% of the nests. These nests had a significantly higher probability to be abandoned during the early stages (until the third incubation day), compared to nests without interactions. Moreover, woodpeckers attacked and made distress calls more frequently in response to the presentation of the starling, compared to predator and non-competing species models. We also documented evidence of joint nesting, as four breeding pairs of woodpeckers shared their nest chamber with starlings. Our results indicate that neotropical woodpeckers are more likely to abandon their cavity when they interact with starlings. Since the starling is expanding quickly in Argentina, this information points at the need to develop management programs to control the impacts of this invasive species on the native fauna, especially on species with conservation concerns.

Keywords: cavity-nesting birds, cavity usurpation, *Colaptes campestris*, *Colaptes melanochloros*, invasive species, neotropical region

Introduction

The European Starling (*Sturnus vulgaris*) (hereafter 'starling'), a cavity nesting passerine, is an invasive species in most of the world and is now found on every continent except Antarctica (Cabe 2020). This species is considered to be one of the hundred 'worst' invasive species in the world (Lowe *et al*. 2000, Santiago-Alarcón and Delgado 2017), mainly because of its competitiveness with native species (Gonzalez-Oreja *et al*. 2018). Several studies have examined the competitive interactions between starlings and native woodpeckers for cavity use (Kerpez and Smith 1990, Mazgajski 2003, Wiebe 2003, Frei *et al*. 2015). In Europe, Mazgajski (2003) reported that the Great Spotted Woodpecker (*Dendrocopos major*) tends to reuse the same cavity every year except after starlings' use, in which case the Great Spotted Woodpecker excavates a new cavity. Kerpez and Smith (1990) found that an increase in the number of starling nests decreases the number of Gila Woodpecker nests (*Melanerpes uropygialis*) in saguaro cacti forests in Arizona, US. Other studies revealed that starlings usurped 52% of the cavities used by the Red-bellied Woodpecker (*Melanerpes carolinus*) in Mississippi, US (Ingold 1989), 10% of the Red-headed Woodpecker's (*Melanerpes erythrocephalus*) in Ontario, Canada (Frei *et al*. 2015), and 7% of the Northern Flicker's (*Colaptes auratus*) in British Columbia, Canada (Wiebe 2003). Given these numbers, strategies to control the starling have been developed and although most are focused on reducing their effect on crops, some of them help to avoid competition with native species (Feare *et al*. 1992, Williams *et al*. 2019).

In an experimental approach, Ingold (1998) located nest boxes in an agricultural woodland in Ohio, US, where Northern Flickers and starlings were present. They found that although cavity supply for the starlings was abundant, they still preferred Northern Flicker cavities and evicted 68% of the flicker pairs from their cavities. Olsen *et al*. (2008) exposed groups of Acorn Woodpecker (*Melanerpes formicivorus*) breeding in a woodland in California, US, to life-like starling models and found that all breeding groups attacked the starling. Furthermore, in Canadian woodlands mixed with open areas, Wiebe (2004) found that, after 40 years of coexistence, most Northern Flicker breeding pairs attacked life-like starling models. Although assessing whether woodpecker species actively perform nest defence behaviours against the starling is important because these behaviours can reduce nest usurpation rate (Wiebe 2004), field experiments are relatively scarce in the literature and non-existent for South America.

Starlings were first recorded in Argentina in 1989 (reviewed in Peris *et al*. 2005), on the eastern coast of Argentina in Buenos Aires city. In the last 15 years the population has increased exponentially (Zufiaurre *et al*. 2016), expanding its range towards the central-eastern part of the country. There have also been observations of starlings in the western and northern regions of Argentina, throughout Uruguay and one record in northern Chile (distribution map provided by www.ebird.org, accessed December 15, 2020). At the study site located in Punta Indio, central-eastern Argentina, starlings were winter visitors, at least until 2004 (Peris *et al*. 2005). The first breeding pair was recorded in 2008, with the species becoming increasingly abundant by 2013 (LS, *unpubl. data*), with ~150 pairs breeding within the study area and flocks of over 100 individuals seen by the end of the breeding season (AJ, *unpubl. data*). To date, there have only been two published reports on South American starling-woodpecker interactions, both on usurpation of Green-barred Woodpecker (*Colaptes melanochloros*) cavities in Argentina (Rebolo Ifran and Fiorini 2010, Ibañez *et al*. 2015).

The starling has expanded quickly throughout the region, which has a potential impact on woodpecker breeding performance, although information on starling-woodpecker interactions is still lacking. Our first objective is therefore to report the competition for cavity use between the starling and two native woodpeckers, the Green-barred Woodpecker and the Campo Flicker (*Colaptes campestris*), in a native semi-open forest of central-eastern Argentina. To do so, we monitored woodpecker cavities systematically to detect interactions between the species. Second, we assess the effect of starlings on woodpecker's breeding performance by comparing the fate of nests with and without starlings' interactions. Given the background research on the starlings' effects on other woodpeckers, we predicted there will be significantly lower nest success for nests with starlings' interactions, compared to nests without interactions. Third, we assess woodpecker's behaviour towards the starlings by presenting life-like starling models to breeding woodpecker pairs. Given the interactions between the starling and the Green-barred Woodpecker in Argentina (Rebolo Ifran and Fiorini 2010, Ibañez *et al*. 2015), and the previous reports of woodpeckers attacking starling models (Wiebe 2004, Olsen *et al*. 2008), we predicted woodpeckers will attack the starling models in contrast to those of other species' that do not compete for cavity use.

Material and methods

Study area and species

We conducted the study at 'Estancia Luis Chico' (35° 20' S, 57°11' W; 8 m a.s.l.), Punta Indio, Buenos Aires province, Argentina. It is a 2000 ha area composed by semi-open forests within a grassland matrix, in which the main tree species are tala (*Celtis tala*) and coronillo (*Scutia buxifolia*). The National Meteorological Service of Argentina reports an average annual temperature of 17º C while annual precipitations range between 850 and 1065 mm. The study site is located within the Flooding Pampas ecoregion, a flat region characterized by abundant rains providing natural hydration to crops.

The Green-barred Woodpecker and the Campo Flicker are two sexually dimorphic mid-sized neotropical woodpeckers which are distributed between north-eastern Brazil and south-western Argentina (Winkler and Christie 2002). Both species use similar sized cavities to lay their eggs (de La Peña 2016, Jauregui 2020), which are mostly excavated by themselves prior to clutch initiation. However, they also re-use cavities from earlier years, which may be older cavities excavated by the same breeding pair, by another breeding pair from either species or, although unlikely, natural cavities (Winkler and Christie 2002, de La Peña 2016). The Campo Flicker can also breed in terrestrial termitaria and forages in open areas while the Green-barred Woodpecker prefers forested areas but may occasionally visit open areas (Winkler and Christie 2002). Both species breed from late September to mid-January. They have clutch sizes of ~4 eggs and will rear ~2 fledglings when successful.

The starling is a mid-sized sexually monomorphic passerine. It is native to Europe and Asia and has been introduced to Africa, North America, Australia and South America (Cabe 2020). The starling is a secondary cavity nesting species and competes with other cavity nesters for cavity use (Kerpez and Smith 1990, Mazgajski 2003, Frei *et al*. 2015). It is an omnivorous species feeding on insects, fruits, and seeds both on the ground and in trees (Cabe 2020). The breeding season of the starling in our study area lasts from mid-September to mid-December (Ibañez 2015).

Field methods

We studied woodpecker breeding biology during the 2015-2016, 2016-2017, 2017-2018 and 2018-2019 breeding seasons. We searched breeding territories by walking every forested area within the farm every 3-4 days, searching intensively throughout the forest. Whenever we detected woodpecker activities (vocalizations, movements, wood pecking sounds, entering/leaving cavities), we assumed there was an active woodpecker nest nearby and searched for cavity entrances. Once we found a nest, we visited it every 2-3 days and monitored the nest. This consisted of checking cavity content (using a mirror and a torch) and observing the nest for 30 min at 40 m distance using binoculars. In each visit, we looked for and recorded starling-woodpecker interactions, which included: (a) direct attacks between the species, (b) species entering the cavity simultaneously (Suppl. Video 1) and (c) cavity sharing events (Suppl. Fig. 1). Previous studies (Wiebe 2003, Frei *et al*. 2015) and our five years of experience monitoring woodpecker nests at the study site, indicate starlings are prone to usurp cavities in the early stages of nesting. Therefore, we monitored the nests and recorded interactions only during cavity construction, egg laying and early incubation stage (*i.e.*, until the third incubation day) (hereafter 'early stages'). We assessed whether starling interactions influenced the likelihood of continuing an ongoing nest attempt. Hence, whenever we observed any of the interactions listed above during the early stages, we classified the nest as 'with interaction', and the other nests were considered 'without interaction'. We also classified nests as either 'abandoned' or 'not-abandoned'. We assumed a nest was abandoned if we did not observe woodpecker activity in the nest surroundings in two consecutive visits (at least three days of inactivity) and not-abandoned if woodpeckers continued with the ongoing breeding attempt.

There were eight nests for which we detected interactions in consecutive visits: six nests during two consecutive visits (four of them abandoned by the woodpeckers) and two nests during three consecutive visits (both abandoned by the woodpeckers). We recorded whether woodpeckers continued the nest attempt during the following monitoring visits.

Nest defence experiments

During the 2018-2019 breeding season, we assessed whether woodpeckers perform nest defence behaviours against the starlings by exposing them to life-like models of: (1) starling; (2) white-eared opossum (*Didelphis albiventris*); and (3) Rufous-bellied Thrush (*Turdus rufiventris*). We considered the white-eared opossum as a predator control, since it is relatively common in the study area and is a woodpecker nest predator (Jauregui 2020). We considered the Rufous-bellied Thrush as a passive control, since it is abundant in the area and of similar size than the starling, but represents no threat to woodpeckers. We conducted the experiments throughout the peak of the starling's breeding season, in October and November (Ibañez 2015). We presented models only during egg laying or early incubation stages (see *Field methods*). We mounted models on a tree branch in an upright position and positioned models to face the cavity entrance at a distance of 1 m (Suppl. Fig. 1). We defined latency as the time elapsed from model presentation to the return of the breeding pair to the nest (*i.e.*, model detection) (Wiebe 2004). We recorded woodpecker responses using a hidden video camera (Sony DCR-HC52) from a 10-15 m distance for the first 5-minute period after model detection (Segura and Reboreda 2012). To control for woodpeckers responding to a particular model, we used two different models of white-eared opossum and three of starling and Rufous-bellied Thrush. Models were installed in a random order with a 20 min interval between each treatment to control for the effect of presentation order (see Segura and Reboreda 2012). While developing the experiments, we were forced to discard four nests, one (Campo Flicker) because a tree climbing snake (*Philodryas patagoniensis*) appeared during the first between-treatment period, and three (two Campo Flicker and one Green-barred Woodpecker) because breeding pairs did not return to the nest.

We classified woodpecker responses according to two criteria. For the first criterion, we classified the 5-minute period after model detection by determining the amount of time (in seconds) invested in: (a) nest defence (< 2 m distance from the model), (b) time inside the cavity, and (c) time far away from the model (> 2 m distance from the model). For the second criterion, we addressed the number of: (a) aggressive attacks to the model; (b) times entering the cavity; and (c) distress calls.

Statistical analysis

To determine whether starling interactions influence the likelihood of continuing an ongoing nest attempt, we used a generalized linear model with a binary response and a logit link function, where '0' = woodpeckers abandoned the nest during the early stages and '1' = woodpeckers did not abandon the nest during the early stages; and the predictor variable was the presence/absence of an interaction with the starling. We used non-parametric Friedman tests to assess whether responses of woodpeckers and latency time differed among treatments. We considered breeding pairs as a blocking factor in all cases. We used this approach due to the absence of normality and variance equality with either original or transformed data. Finally, we used a Wilcoxon sum-rank test to assess latency differences between the woodpeckers. Analyses were performed in R 3.6.3 (R Development Team 2020) using the package 'agricolae' (de Mendiburu 2020). Values presented are mean ± SE.

Results

We monitored 36 nests of the Campo Flicker and 72 of the Green-barred Woodpecker and detected interactions with starlings in seven of the Campo Flicker nests and five of the Green-barred Woodpecker nests. We registered woodpeckers attacking starlings at cavity entrances (n = 4 nests), starlings flushing from an active woodpecker cavity when we approached the nest (n = 2 nests) (Suppl. Video A1), starlings entering the cavity during visits (n = 2 nests), and both woodpeckers and starlings laying their eggs simultaneously in the same nest chamber (n = 4 nests, Suppl. Table 1, Suppl. Fig. 2). Of these four joint nesting cavities, the woodpeckers abandoned three with the starlings continuing the nesting attempt, and the starlings abandoned one with the woodpeckers continuing the nesting attempt. In total, after an interaction with starlings, seven breeding pairs (58%; four of the Campo Flicker and three of the Green-barred Woodpecker) abandoned their nests, while the rate of abandonment was 18% for nests without interaction. We found that the odds of continuing the nesting attempt decreased significantly when there was an interaction with the starling (β = -0.33 ± 0.58, P = 0.003, n = 108; Fig. 1). All cavities abandoned after an interaction were then used by starlings.

We presented models to six Campo Flicker and 13 Green-barred Woodpecker pairs (n = 19 nests) (Table 1) and the only model attacked by the woodpeckers was the starling (17 of the 19 breeding pairs attacked the starling, range = 1-25 attacks; Tables 1 and 2). Other responses included distress calls to the starling (only made by the Green-barred Woodpecker) and the opossum (by both species) models, but not to the thrush model (Table 2). Woodpeckers invested more time inside the cavity and entered it a greater number of times when exposed to either the starling or the thrush models (Table 2), compared to the opossum. The Green-barred Woodpecker spent more time far from the nest when exposed to the opossum model (Table 2). Latency was 4.7 ± 0.6 min for the Green-barred Woodpecker and 6.9 ± 1.4 min for the Campo Flicker. There was no significant latency difference between the woodpecker species (W = 408, P = 0.33) nor among treatments for each species (Green-barred Woodpecker: χ^2 = 0.27, P = 0.87; Campo Flicker: χ^2 = 5.33, P = 0.07).

Discussion

We provide the first report of interactions between the starlings and two native neotropical woodpeckers in a natural habitat of central-eastern Argentina. Our results show that the starlings compete with the woodpeckers for cavity use. Woodpeckers' abandonment rate after an interaction with the starlings (58%) was greater than those reported in North America for the Lewis Woodpecker *Melanerpes lewis* (4 %; Vierling 1997) and the Red-headed Woodpecker (36%; Frei *et al*. 2015). These two species may perform more aggressive behaviours to achieve cavity retention against the starling compared to the species we studied (Wiebe 2004), which could explain the difference. As the starling propagation in Argentina is recent, our woodpeckers may need more time to develop such behaviours. Because of our monitoring methodology, we cannot discard the possibility that there were breeding pairs that retained the cavity after an unobserved interaction. However, some cavities might have been abandoned before clutch initiation due to an undetected interaction (AJ, *unpubl. data*). We are confident that the observed interactions caused cavity abandonment by the woodpeckers, and hence, we believe that patterns would hold with a greater observation time. Cavity abandonment is detrimental for woodpeckers. On the one hand, nest abandonment after clutch initiation implies they invested in a brood they will not raise. On the other hand, starlings occupy many cavities that are, consequently, unavailable for woodpeckers (AJ, *unpubl. data*), and also usurp cavities before clutch initiation. In most cases, woodpeckers have to either excavate or find another suitable cavity to lay their eggs, with the problem that there are fewer cavities available because of starling presence. This could eventually be more detrimental if the usurpation occurs in the second half of the breeding season, when woodpeckers' nest survival decreases (Jauregui 2020). As there is evidence that at least two breeding pairs re-nested in the same territory after cavity usurpation (Jauregui 2020), woodpeckers are probably able to, at least in part, overcome the starling presence in their current numbers.

Our study reports the first records of woodpeckers laying eggs with another species, here the starling, simultaneously in the same nest chamber. Cavity sharing has rarely been reported (Robinson *et al*. 2006, Cornelius *et al*. 2008, Cockle 2010, Lammertink *et al*. 2019) and reports comprise either two secondary cavity nesters rearing broods independently (Robinson *et al*. 2006, Cornelius *et al*. 2008) or species using the cavity for different purposes (a woodpecker roosting and a parakeet or a woodcreeper pair breeding; Cockle 2010, Lammertink *et al*. 2019). In every sharing event we monitored, one of the species ended up abandoning the cavity after egg laying. Hence, this is probably a result of both species trying to use the cavity, in which both lay their eggs but one of them ends up abandoning. We also noted that starlings used an additional 30 inactive woodpecker cavities during the span of our study (AJ, *unpubl. data*), so there might be a shortage of natural cavities which drives competition between the species (Cornelius *et al*. 2008, Cockle 2010) or starlings may prefer woodpecker cavities (Ingold 1998). The three nests abandoned by woodpeckers after cavity sharing had one, two and three woodpecker eggs (for completed clutches, modal clutch size of both species is four eggs; Winkler and Christie 2002, Jauregui 2020). Reduced clutch size could be a consequence of fights inside the cavity (causing egg breakage), of woodpeckers abandoning the cavity before completing the clutch or due to woodpeckers' own egg rejection after interacting with the starling (Suppl. Video A1).

Furthermore, only one woodpecker egg hatched in the non-abandoned nest (modal number of nestlings of both species is three nestlings; Winkler and Christie 2002, Jauregui 2020). The number of eggs inside the cavity may lead to incubation deficiency, which would explain the hatching of only one egg in the non-abandoned nest.

As predicted, woodpeckers responded aggressively to the starling model, most likely recognizing it as a nest competitor. Aggressive behaviours could reduce nest usurpation rate (Wiebe 2004), hence, usurpation rates could be greater than suggested by our results if there was no such behaviour. Most animals need prior experience before learning to react to threats (Mirza *et al*. 2006, Reudink *et al*. 2007). Therefore, since the starling has been present in this study area for 15 years (Peris *et al*. 2005), woodpecker's responses might be caused by prior interactions during this short time period (Wiebe 2004). It is also possible that these behaviours have an innate component, as suggested for the Northern Flicker (Wiebe 2004), which would imply woodpeckers do not need prior experience against a threat to develop such behaviours. These two possibilities are not exclusive. Woodpeckers could have an innate nest defence behaviour against all nest competitors and have learned that the starling is a nest competitor, hence, they attack it. Future studies should focus on the responses of woodpeckers in areas where the starling is not yet present (such as northern and southern Argentina) to help contribute to the understanding of these mechanisms. We also noticed breeding pairs demonstrated a high variation in the number of attacks on starlings. Behaviour may be modified with experience (Wiebe 2004) and birds gain experience as they age (Hatch 1997). However, Fisher and Wiebe (2006) found that Northern Flicker defence behaviour did not change with age. It may be that pairs that attacked more times had a greater number of previous interactions with starlings (*e.g.* they tried to use the same cavity or compete for feeding resources during winter or the starling tried to usurp a cavity the previous breeding season) compared to less aggressive pairs.

Our study on these two woodpeckers represents the first that quantifies, with both empirical and experimental data, the negative impact the starlings cause on the neotropical native fauna. Starlings are generating an extra cost to native woodpeckers (see also Kerpez and Smith 1990, Mazgajski 2003, Wiebe 2003), not only by disturbing them during the nesting process, but also by causing an increase in nest abandonment rate (Frei *et al*. 2015). This information is crucial for conservation purposes because it helps us understand its impact and plan future actions to control this invasive species. The Green-barred Woodpecker and the Campo Flicker are two abundant species and may overcome the 6% abandonment rate caused by starlings by re-nesting during the same season, although this should be monitored. However, starlings are expanding quickly (Zufiaurre *et al*. 2016), being a highly adaptable species (Lowe *et al*. 2000) that causes several problems to the native fauna (Ingold 1989, Lowe *et al*. 2000, Wiebe 2003, Frei *et al*. 2015). Hence, special attention and care should be taken if the starling reaches areas (such as the northeast of Argentina) with numerous endangered native cavity nesting species (Bonaparte *et al*. 2020) which could be specially threatened by the starlings' usurpation and aggressive behaviours.

Declarations

Geolocation information. Punta Indio, Buenos Aires, Argentina (point): 35°20′S, 57°11′W.

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Supplementary material

Supplementary Video 1. Record of a starling-woodpecker interaction at a Campo Flicker nest that had one Campo Flicker egg inside. Part A: a starling adult enters the cavity and a Campo Flicker male arrives immediately after. When the Campo Flicker approaches the cavity, it detects the starling inside and tries to flush it away from the cavity, unable to succeed. Part B: after the first interaction, the male returns to the cavity (starling was no longer inside) and seconds later it takes away its own egg.

Supplementary Figure 1. Life-like models used to assess both Campo Flicker and Green-barred Woodpecker responses to: (a) white-eared opossum; (b) European Starling; (c) Rufous-bellied Thrush. Red arrows point to cavity entrances and green arrows point to models.

Supplementary Figure 2**.** Cavity chamber contents indicating interaction between the Green-barred Woodpecker or the Campo Flicker with the European Starling in a native forest of central-eastern Argentina. Panels represent: (a) four starling eggs and one Campo Flicker egg; (b) four starling eggs and three Green-barred Woodpecker eggs; (c) three starling eggs and two Campo Flicker eggs.

Supplementary Table 1. Events of nest chamber sharing between the European Starling with either the Campo Flicker or the Green-barred Woodpecker in a native forest of central-eastern Argentina. Events represent changes in nest content or stage and are not consecutive visits.

Figure 1. Probability of woodpeckers continuing a nesting attempt into the early stages (while they are excavating the cavity, laying their eggs, or starting the incubation) as a function of the presence/absence of interactions with starlings. Plotted mean probability ± 95% confidence intervals.

Table 1. Responses of the Green-barred Woodpecker and Campo Flicker to model presentations in a native forest of central-eastern Argentina. Time units are seconds while direct aggressions, distress calls and number of times entering the cavity are frequencies.

Treatment	Response	Green-barred Woodpecker (*n* = 13 nests)	Campo Flicker (*n* = 6 nests)
European Starling	Time inside the cavity	51.7 ± 22.5	85.2 ± 36.4
	Time close to model	235.2 ± 25.5	161.2 ± 40.7
	Time far from model	13.1 ± 10.3	53.6 ± 16.2
	Direct aggression	10.4 ± 2.6	6.2 ± 4.3
	Distress calls	21.1 ± 6.6	0.0 ± 0.0
	Times entering cavity	0.7 ± 0.3	1.0 ± 0.4
White-eared opossum	Time in the cavity	0.0 ± 0.0	0.0 ± 0.0
	Time close to model	165.4 ± 29.9	188.5 ± 39.9
	Time far from model	134.6 ± 29.7	111,5 ± 39.9
	Direct aggression	0.0 ± 0.0	0.0 ± 0.0
	Distress calls	19.8 ± 11.4	35.0 ± 15.5
	Times entering cavity	0.0 ± 0.0	0.0 ± 0.0
Rufous-bellied Thrush	Time in the cavity	81.3 ± 32.4	90.6 ± 49.9
	Time close to model	128.5 ± 27.2	89.5 ± 43.0
	Time far from model	90.2 ± 30.6	119.9 ± 46.9
	Direct aggression	0.0 ± 0.0	0.0 ± 0.0
	Distress calls	0.0 ± 0.0	0.0 ± 0.0
	Times entering cavity	0.4 ± 0.2	0.7 ± 0.3

Table 2. Statistical analyses (Friedman test) for each recorded variable and comparisons among treatments for the Campo Flicker and the Green-barred Woodpecker in 2018-2019 breeding season. Significant differences at P < 0.05. Op = white-eared opossum; Th = Rufous-bellied Thrush; St = European Starling.

Variable	Campo Flicker (*n* = 6 nests)		Green-barred Woodpecker (*n* = 13 nests)	
	Friedman test	Comparison	Friedman test	Comparison
Time inside the cavity	χ^2 = 5.92, P = 0.04	Op < Th & St	χ^2 = 9.48, P < 0.01	Op < Th & St
Time close to model	χ^2 = 2.69, P = 0.25	St = Th = Op	χ^2 = 3.36, P = 0.18	St = Th = Op
Time far from model	χ^2 = 1.65, P = 0.44	St = Th = Op	χ^2 = 8.84, P = 0.01	St & Th < Op
Direct aggression	χ^2 = 8.00, P = 0.02	Op & Th < St	χ^2 = 26.00, P < 0.01	Op & Th < St
Distress calls	χ^2 = 6.00, P = 0.04	Th & Op < St	χ^2 = 8.00, P = 0.02	Th < Op & St
Cavity visits	χ^2 = 5.97, P = 0.04	Op < Th & St	χ^2 = 7.76, P = 0.02	Op < Th & St