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Breeding southern house wrens exhibit a threat-sensitive response when exposed to different predator models

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Abstract We assessed the ability of southern house wrens (*Troglodytes aedon musculus*) to recognize and discriminate different birds of prey. We exposed nesting birds to stuffed specimens of two sympatric predator species, the chimango caracara (*Milvago chimango*, a nest predator) and the roadside hawk (*Buteo magnirostris*, a predator of adults and nests), and to a dummy of a non-sympatric predator, the double-toothed kite (*Harpagus bidentatus*, a predator of adults). Nesting wrens avoided going into their nest or took a longer time to resume their parental duties when exposed to the predators than when they were exposed to a control dummy (*Chrysomus ruficapillus*, a sympatric blackbird). Nest avoidance was higher when birds were exposed to the roadside hawk but no differences were detected when exposed to the chimango caracara or the double-toothed kite. The results indicate that southern house wrens are able to recognize a predator, responding in a graded manner. Our findings support the hypothesis that southern house wrens exhibit a threat-sensitive response during breeding. Also, individuals were able to recognize the unknown predator but failed to correctly assess the threat level represented by it. We propose that correct assessment of threat level by house wrens requires direct experience with the predator, which might mediate in the modulation of the response.

Introduction

Predator recognition is an important component of antipredator defense mechanisms in preys and constitutes the basis for the development of other antipredator strategies (Curio 1976; McLean and Rhodes 1991). Correct recognition of the threat represented by the predator can result in a rapid and specific response of preys that allows them to reduce their predation risk (Chivers and Mirza 2001; Chivers and Smith 1998). However, responding to threats also entails costs for preys, such as lost opportunities for foraging and mating (Lima and Dill 1990; Lima 1998). This trade-off between benefits of reduced risk and fitness-related costs could be optimized by preys by exhibiting a threat-sensitive response (Helfman and Winkelman 1997; Ferrari et al. 2008). This response involves the alteration of prey avoidance behaviors in a manner that reflects the magnitude of the predator threat (Helfman 1989). As defined, such threat-sensitive response is dependent on the ability of prey to assess the degree of threat presented by a predator, and it implies that the prey response will match the potential danger imposed by the predator (Webb 1982; Helfman and Winkelman 1997; Ferrari et al. 2008). The alternative to a threat-sensitive response is a nongraded all-or-nothing response to the detection of a predator (Sih 1987; Lima and Dill 1990; Curio 1993).

The threat-sensitivity predator avoidance hypothesis has received support from several studies in a broad range of taxa, including birds (e.g., Johnson et al. 2003; Edelaar and Wright 2006; MacLean and Bonter 2013; Turney and Godin

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2014; Królikowska et al. 2016). Recent studies suggest that preys might use a generalized predator recognition system by extending the antipredator response displayed when exposed to known predators to other morphological similar or closely related novel predators (Griffin et al. 2001; Ferrari et al. 2007; Stankowich and Coss 2007). Generalized predator recognition has been suggested to be a specific case of stimulus generalization, where the response to a conditioning stimulus is generalized to other, similar stimuli. In that sense, the generalized recognition system requires that individuals recognize specific characteristics of predators and use them to target novel predators as dangerous (Ferrari 2009). Such a recognition system would be highly adaptive, as it provides individuals with a low-cost way to avoid novel predators with no prior experience of the threat (Griffin et al. 2001).

Here, we test the ability of the southern house wren, *Troglodytes aedon musculus*, to recognize predators and respond in a graded manner. We also assess whether southern house wrens are able to generalize this threat recognition to other related novel threats. We use the term "recognition" to indicate the capacity of individuals to correctly classify objects or other animals based on some typical features (Shettleworth 2010; Beránková et al. 2015). During the nesting cycle, house wrens faced with a threat avoid entering the nest, reducing risk taking, and emit alarm calls (Fasanella and Fernández 2009; Fernández and Llambías 2013; Fernández et al. 2015). In this study, we assessed the response of breeding house wrens to two different bird of prey stuffed specimens (one an adult bird predator and one common nest predator) and to a non-threatening passerine dummy. We expected that, if house wrens are able to recognize their predators and exhibit a threat-sensitive response, they should display the strongest nest-avoidance and alarm-calling response when exposed to the stuffed adult bird predator, but show a weaker response to the nest predator and the nonthreatening species dummy. Lastly, we exposed the breeding house wrens to a dummy model of a non-sympatric adult predator, a novel species that does not coexist with the house wren in the study area and that can prey on adults. We predict that, if wrens are able to generalize the recognition of one predator to other closely related novel species that may represent a threat, then when exposed to this novel nonsympatric bird of prey, the response of southern house wrens should be similar to when exposed to a sympatric adult predator.

Materials and methods

We studied a southern house wren population inhabiting an 8-ha forest patch near General Lavalle (36° 20′S, 56° 54′O), Buenos Aires Province (Argentina), during the 2004–2006

and 2010 breeding seasons. The study site is a coastal woodland composed mainly of *Celtis ehrenbergiana*, *Scutia buxifolia*, and *Schinus longifolius*. At this site, there were 106 nest-boxes attached to trees, 1.5 m above the ground, that house wrens use regularly for nesting (Carro et al. 2014). The mean number of nests surveyed in this area during the study period (2004–2006 and 2010) was 40.25 (range 23–56), and the mean number of breeding pairs was 28.5 (range 18–37).

The southern house wren is a small (12 g) insectivorous passerine distributed in America from eastern Oaxaca (Mexico) to Tierra del Fuego (Argentina). This species is monochromatic and apparently monomorphic, with males defending a territory by singing. These birds usually nest in natural and artificial cavities. Its breeding season in central Argentina extends from October to January, and at our study site, southern house wrens are territorial, socially monogamous, and resident all year round. The clutch size in this species is typically 4–5 eggs, and only the female incubates the eggs for 14–15 days. Both parents rear the nestlings for 15–17 days, but brooding of nestlings is performed only by the female (Skutch 1953; Young 1994; Llambías and Fernández 2009; Llambías et al. 2015). The parental care roles of southern house wrens vary during the nestling rearing stage. Typically, early in the nestling rearing cycle, the male performs most of the nest feeding visits whereas the female broods the chicks. Brooding decreases up to a near cease when the nestlings are 6–7 days old, and the female increases its contribution to feeding nestlings after this period (Llambías et al. 2012).

Once nesting had begun, we monitored the nests every other day and recorded the clutch size, brood size, and hatching date. We captured and banded nesting birds using mist-nets prior to the start of the breeding attempt or when nestlings were 10–11 days old using a wig-wag trap at the box. Captured birds were banded with unique combinations of a numbered aluminum ring and three plastic color bands.

Experimental design

Initially, during the 2004–2006 breeding seasons, we exposed nesting house wren pairs to one stuffed specimen of each one of a chimango caracara (*Milvago chimango*), double-toothed kite (*Harpagus bidentatus*) or a chestnut-capped blackbird (*Chrysomus ruficapillus*). Stuffed specimens have been shown to be more adequate than other dummy models when testing bird responses to predators (see Němec et al. 2015). During 2010, we exposed nesting wrens to a stuffed specimen of a roadside hawk (*Rupornis magnirostris*) (Fig. 1). The chimango caracara and the roadside hawk are common birds of prey in our study site. The chimango caracara is a dietary opportunist. Main items in its diet are provided by carrion, although it

Fig. 1 Stuffed specimens used in the experiments: **a** chestnut-capped blackbird, **b** chimango caracara, **c** roadside hawk, and **d** double-toothed kite

also feed on invertebrates, amphibians, reptiles, and small rodents (Yáñez and Núñez 1980; Tobar et al. 2015). It is also a known predator of eggs and nestlings (Fraga and Salvador 1986; Donázar et al. 1996; Mezquida and Marone 2003; Vergara 2007; Salvador 2016), and it has been identified as one of the most important nest predators of house wrens and the thorn-tailed rayadito (*Aphrastura spinicauda*) nesting in nest-boxes in central Chile (Vergara 2007). Thus, we assumed that the chimango caracara represents a nest threat for nesting house wrens. The roadside hawk and the double-toothed kite present similar feeding habits. Both are generalist raptors that prey upon invertebrates, reptiles, amphibians, small mammals, and birds (Panasci 2013; Schulze et al. 2013). Their diets vary spatially and seasonally, probably according to prey availability. A number of studies have noted predation of small birds by roadside hawks (Young 1929; Dickey and van Rossem 1938; Howell 1972; Belton and Dunning 1982;

Panasci and Whitacre 2000; Brightsmith 2002; Di Giacomo 2005), although some studies also reported predation upon eggs, nestlings, and fledglings (Young 1929; Brown and Amadon 1968; Groom 1992; Liljesthröm et al. 2014; Salvador 2016). We also observed one predation attempt of a roadside hawk on a nesting house wren in a population near our study area, as it left the nest-box. Based on this evidence, we considered that the roadside hawk presumably represents a serious threat to nesting house wren adults and their nests. The double-toothed kite represents a novel, non-sympatric predator, whose distribution range extends from Mexico to Southern Brazil and eastern Bolivia but does not include Argentina (Brown and Amadon 1968). Therefore, house wrens in our study area have no previous experience with this bird of prey. Double-toothed kites prey upon insects, small amphibians, and reptiles, as well as on small passerines (Baker and Whitacre 1999; Schulze et al. 2000). Finally, the chestnut-capped blackbird is a

nonthreatening species that inhabits marshes and open humid areas in our study area, and is a reliable control dummy (see "Results").

We carried out the experiments during the austral breeding season (October–December). We only included the first broods with a typical number of nestlings (4–5 nestlings) in our experiments to reduce possible variability generated by differences in brood size. We performed all experiments in the morning (0600–1100 h), and the treatment applied to each nest was selected at random. We performed a total of 89 experiments exposing nesting birds to dummy models: 23 to the chimango caracara dummy, 18 to the roadside hawk, 28 to the double-toothed kite, and 20 to the control dummy. Each breeding pair ($n = 76$) was exposed once to any dummy specimen to avoid habituation, but some nests ($n = 13$) were exposed to two different dummies, each one at a different nesting stage.

We carried out the experiments at two different times during the nesting period: (1) early nestling rearing stage (when nestlings were 3–4 days old), or (2) late nestling rearing stage (when nestlings were 9–11 days old). Before exposing breeding pairs to the dummies, we recorded undisturbed parental activity at the nest for 1–1.5 h (pre-exposure period). After this period, we placed the dummy on top of a pole 1.5–1.7 m high, approximately 3 m away from the front of the box, facing the nest-box entrance, and recorded the parental activity at the nest for 0.5 h (exposure period). We video-recorded all sessions using either a Hi8 or a Digital Dcr-Sr85 Sony video camera (Sony Corp., Tokyo, Japan). We covered the video cameras with camouflaged cloth and concealed these by pulling surrounding grass over the top and sides. We placed cameras 8–10 m from the nest 1 h before the beginning of the trials.

We evaluated parental response to the dummies from video-recordings (no observer was present during the experiment). We measured the risk taken by parents by recording the amount of time elapsed from the time the dummy was placed until an adult resumed feeding (latency) (Dale et al. 1996). We also evaluated the variation in parental activity due to the presence of each dummy by comparing the total number of nest visits per hour made by parents when exposed to the stuffed specimens. Finally, we measured the calling response of breeding adults. Southern house wrens usually make alarm calls when facing predators (Fasanella and Fernández 2009). These calls are typified as type I and type II alarm calls based on their emission characteristics. Type I alarm calls are high-frequency calls (frequency peak: 6 kHz) with duration of 400–600 ms, whereas type II calls are low-frequency calls (frequency peak: 3 kHz), shorter in duration (<100 ms) (Corral et al. 2012). Although specific functions of these calls are unknown, it was suggested that type I calls are related to a mobbing function, while type II are given to alert mates or nestlings to the presence

of a threat (Fasanella and Fernández 2009; Fernández et al. 2012). In our experiments, we identified the alarm calls given by the nesting individuals during the first 10 min after being exposed to the stuffed specimen and recorded whether breeding birds uttered type I and/or type II calls during the exposure.

Data analyses

All analyses were performed in the R environment (v3.3.0, R Core Team 2016). Because the experiments with different dummies were carried out during different breeding seasons, we validated the comparison of the wren's response to stuffed models by assessing their response to a plastic great horned owl (*Bubo virginianus*) model (Dalen Gardeneer 16-Inch Molded Owl #OW6; Dalen Products Inc.) used for another experiment during the same breeding seasons (2004–2006 and 2010). No effect of year was detected on either the latency to resume parental activities ($p = 0.4$ and $p = 0.43$ for females and males, respectively) or the changes in parental visits during model exposure ($p = 0.40$ and $p = 0.84$, for females and males, respectively). Thus, we did not include year as a factor in later analyses.

To measure the response of nesting house wrens to the stuffed specimens we measured: (1) the time taken for the birds to return into their nest after placing stuffed specimens (latency), (2) how often the parents visited their nest (after resuming their activities) while the dummies were present, and (3) the alarm calls made by the birds.

In all the analyses, we included the nestling rearing stage, the sex of individuals, and the dummy used (including the nonsympatric stuffed model) as predictors. We also included second- and third-order interactions. Nest identity was included into these models as a random factor.

Cox proportional hazards mixed regression models (COXME package, v2.7.1, Therneau 2015) were used to compare the latency of males and females to go into their nest after we placed the stuffed/control specimens. We included in the analysis the latency to resume parental activities during the preexposure period immediately after we placed the video camera as a control. Therefore, preexposure was included as another additional level into the dummies used. Trials where parents did not return after the exposure to the dummies (maximum latency) were considered as censored.

Parent nest visitation rates when nests were exposed to the dummies were compared using general linear mixed models (lme4 package; Bates et al. 2015). The response variable in these models was the change in the number of male and female nest visits, defined as the ratio between the difference in the number of parent visits to the nest recorded during the pre-exposure and the exposure period, and the number of nest visits made during the pre-exposure period.

The probability of nesting house wrens uttering type I and type II alarm calls when exposed to the different stuffed specimens was modeled using generalized linear mixed models (lme4 package; Bates et al. 2015). We analyzed the probability of breeding birds uttering type I and type II alarm calls separately. We assumed a binomial error distribution and a logit link function. In these models we did not include the sex of the individual as a predictor, as it was not possible to identify the sex of the caller. The response variable was dichotomized according to whether nesting individuals performed alarm calls. We did not analyze the number of calls or the time spent uttering alarms, because they had strongly zero-inflated distributions and no reliable model could be fit.

For each analysis, we used residual and normal probability plots to check model assumptions. Models were reduced by removing all nonsignificant terms. We tested the global contribution of each predictor to the response of nesting house wrens by comparing the deviance of nested models (i.e., with and without the factor) using the likelihood ratio test. Pairwise post hoc comparisons among levels for each significant factor were performed using Tukey honest significant difference (Tukey HSD) tests with the Multicomp R package (Hothorn et al. 2008). All p values quoted are two-tailed, and differences were considered significant at $p < 0.05$.

Results

Predator recognition

In 24.6 % ($n = 15$) of trials, the members of the breeding pair refused to enter the nest following exposure to the dummies. The minimal model explaining the latency to resume parental activities included only the sex of the parent and the dummy model used. Females resumed parental activities before males ($\chi^2 = 23.79$, df = 1, $p < 0.01$; Fig. 2). Females returned to the nest before males in 31 opportunities, while males returned sooner than females in 15 trials. Twelve breeding pairs refused to enter the nest when exposed to the roadside hawk dummy, whereas only three refused to enter the nest when exposed to the chimango caracara, and none when exposed to the chestnut-capped blackbird.

Responses of nesting wrens varied with the stuffed specimen to which they were exposed ($\chi^2 = 128.29$, df = 4, $p < 0.01$). Nesting house wrens took longer to resume nesting activities when exposed to the predators than when exposed to the control species and than during the preexposure period (Table 1; Fig. 2). Furthermore, the latency to return to the nest was higher when exposed to the roadside hawk than when exposed to the chimango caracara (Table 1; Fig. 2).

In those cases where at least one parent returned to the nest when exposed to the predator dummy, the nest visitation rate of parents did not vary with the stuffed specimen used ($\chi^2 = 2.21$, df = 3, $p = 0.53$), the nesting period ($\chi^2 = 0.99$, df = 1, $p = 0.31$), or the sex of the parent ($\chi^2 = 1.81$, df = 1, $p = 0.18$; Fig. 3).

Alarm calling of breeding wrens varied with the nesting period ($\chi^2 = 8.01$, df = 1, $p < 0.01$ for type I alarm calls, and $\chi^2 = 12.36$, df = 1, $p < 0.01$ for type II alarm calls). Wrens uttered type I and type II alarm calls more frequently at late nestling rearing stage than earlier (Fig. 4). Also, alarm calling varied with the stuffed specimen used in the experiments ($\chi^2 = 20.44$, df = 3, $p < 0.01$; Fig. 4). Type II alarm calls were uttered more frequently when exposed to predator dummies than when exposed to the control dummy (Table 2, Fig. 4b).

Wrens also used different calls when exposed to different predator dummies. Breeding house wrens uttered type I alarm calls more frequently when exposed to chimango caracara than when they were exposed to the roadside hawk dummy model (Table 2; Fig. 4a). Instead, when exposed to the roadside hawk model, breeding house wren uttered more frequently type II alarm calls (Table 2; Fig. 4b).

Responses to the novel predation threat

The breeding pair refused to enter the nest in only one of 28 trials with the double-toothed kite dummy. Latency to return to the nest of nesting house wrens when exposed to the double-toothed kite was similar to that observed in nesting wrens when exposed to the chimango caracara dummy but higher than that observed with the chestnut-capped blackbird and lower than that recorded in the experiments with the roadside hawk dummy (Table 1; Fig. 2).

Changes in nest visitation rates of nesting house wrens when exposed to the double-toothed kite were similar to those recorded when nests were exposed to the other dummies ($p > 0.09$ for all comparisons; Fig. 3).

The probability of uttering type I alarm calls and the time calling when exposed to the double-toothed kite dummy did not differ from those when exposed to the control or to the other predator dummies (Table 2; Fig. 4a). When exposed to the double-toothed kite dummy, house wrens uttered type II alarm calls more frequently than when exposed to the control dummy, but similar to when exposed to the chimango caracara (Table 2). Also, the frequency of type II alarm calling was lower when exposed to the novel predator than when exposed to the roadside hawk (Table 2).

Fig. 2 Latency to return to nest for nesting house wrens when parents were exposed to threatening and nonthreatening birds dummies. The threatening birds are represented by two sympatric predator dummies (roadside hawk and chimango caracara) and one nonsympatric predator dummy (double-toothed kite). The nonthreatening bird is represented by a sympatric nonpredator dummy (chestnut-capped blackbird, control for the experiment). Also, the latency to return to the nest of wrens once the video-camera was installed (in absence of any model) is presented. Dots represent median values, boxes the 25–75 % quartile range, and vertical lines the total range of values observed. **a** Female responses; **b** male responses
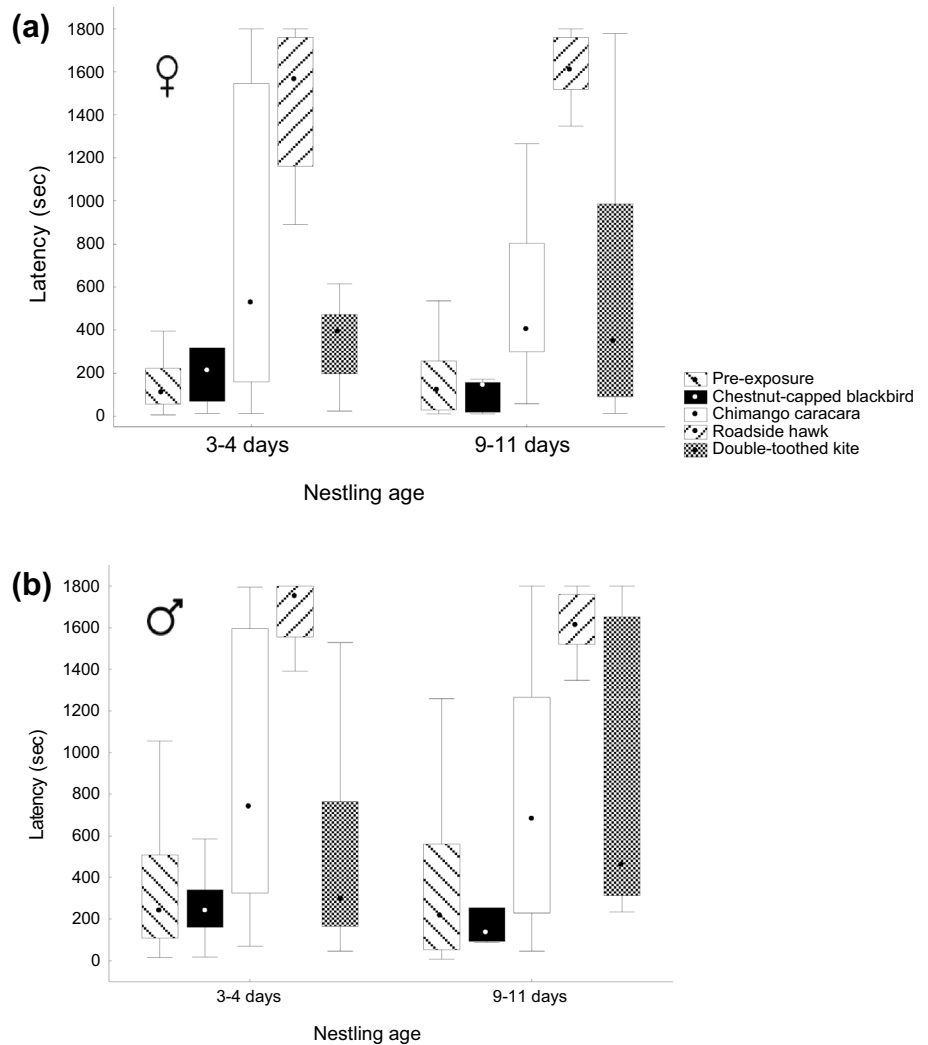
Table 1 Comparison of latencies to return to the nest of house wrens when exposed to a control dummy model (chestnut-capped blackbird) or sympatric predator dummy models (chimango caracara or roadside hawk)

Dummy model	Preexposure period	Chestnut-capped blackbird	Chimango caracara	Roadside hawk
Chestnut-capped blackbird	0.32	–	–	–
Chimango caracara	5.54**	4.11**	–	–
Roadside hawk	7.76**	6.89**	4.11**	–
Double-toothed kite	4.84**	3.23**	1.37	5.16**

Off-diagonal values represent the *z*-statistics of pairwise post hoc Tukey HSD tests

* $p < 0.05$; ** $p < 0.01$

Discussion

Our results suggest that the presence of a stuffed predator model close to the nest elicits an avoidance response in nesting house wrens. When exposed to either the chimango caracara or the roadside hawk dummy, parents took a longer time to resume parental activities or avoided entering the nest throughout the period of exposure to the predator than to the harmless blackbird, and often emitted alarm calls. Except for alarm calling, the responses did not vary with the

Fig. 3 Relative change in parent's nest visitation rate (NVR) during exposure to stuffed specimens of a chestnut-capped blackbird, a roadside hawk, a chimango caracara, and a double-toothed kite. The change was calculated as: (NVR during pre-exposure period – NVR during the exposure period)/ NVR during the pre-exposure period. Dots represent median values, boxes the 25–75 % quartile range, and vertical lines the total range of values observed. **a** Female responses; **b** male responses
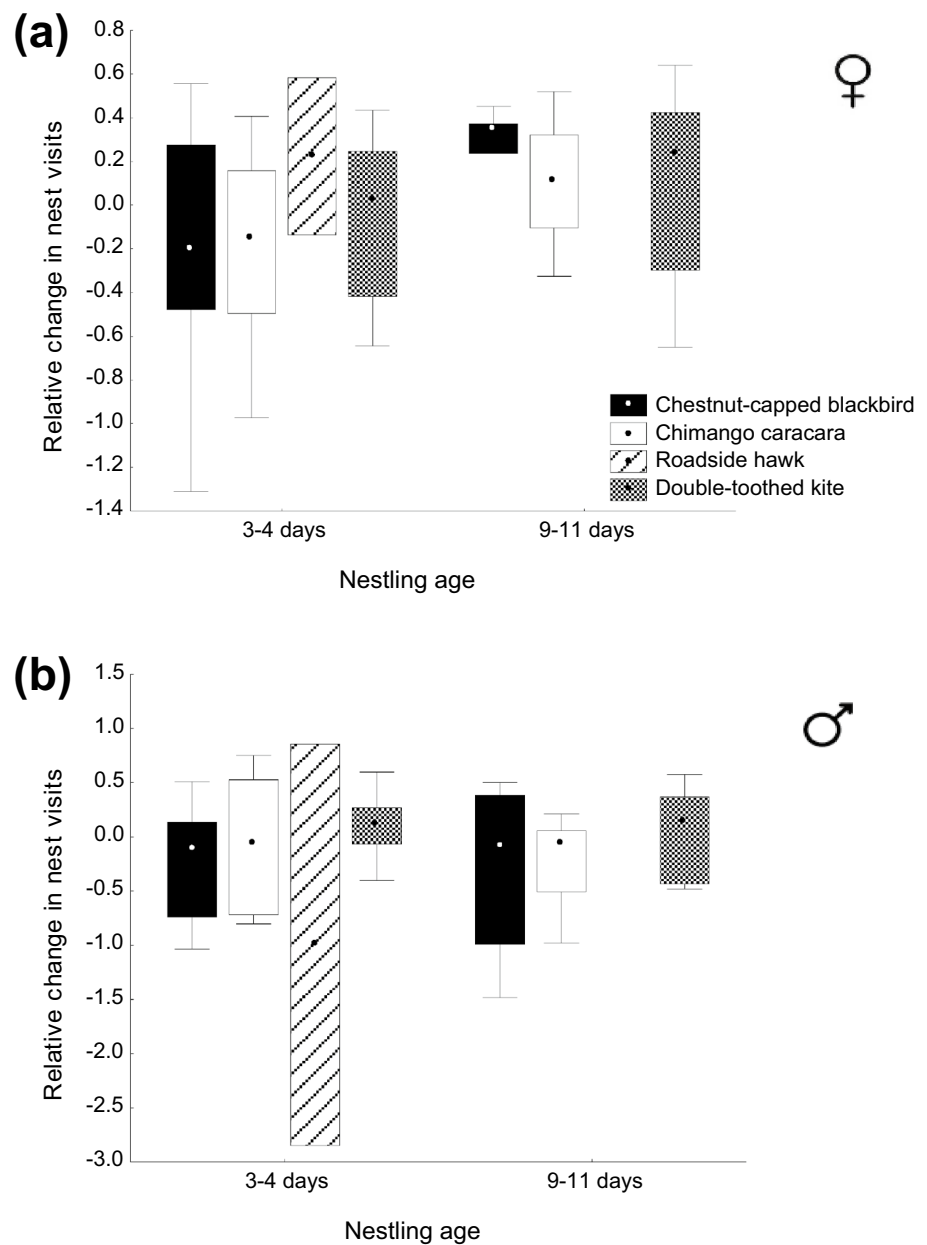
nestling rearing stage, implying that the response is model dependent rather than being related to the value of the brood or the relative harm from which the offspring would suffer in the absence of parental care (Dale et al. 1996).

There is considerable evidence that birds are capable of recognizing a predator (Curio 1975; Owings and Coss 1977; Curio et al. 1983; Hobson et al. 1988; Veen et al. 2000; Göth 2001; Kullberg and Lind 2002; Csermely et al. 2006; Tvardíková and Fuchs 2012; Marzluff et al. 2015; Beránková et al. 2015; Mitchell et al. 2015; Carlson et al. 2017a). Furthermore, this recognition could involve fine-scale discrimination among different predators based on different morphological characteristics when they are from different taxa or when they differ in size (Curio 1975;

Buitron 1983; Curio et al. 1983; Palleroni et al. 2005; Templeton et al. 2005; Strnad et al. 2012; Suzuki 2012; Beránková et al. 2015). Accordingly, we found differences in the response given by breeding house wrens when faced with the chimango caracara and the roadside hawk dummies, which may be related to the level of threat that the dummies represent. Whereas chimango caracaras are nest predators that can eat eggs or nestlings, roadside hawks can prey also on adult individuals and, therefore, represent a higher risk for adult house wrens. In this study, we found that the antipredator response of wrens was stronger when faced with the roadside hawk dummy than with the chimango caracara. When exposed to the roadside hawk, nesting wrens avoided going into the nest in most of the
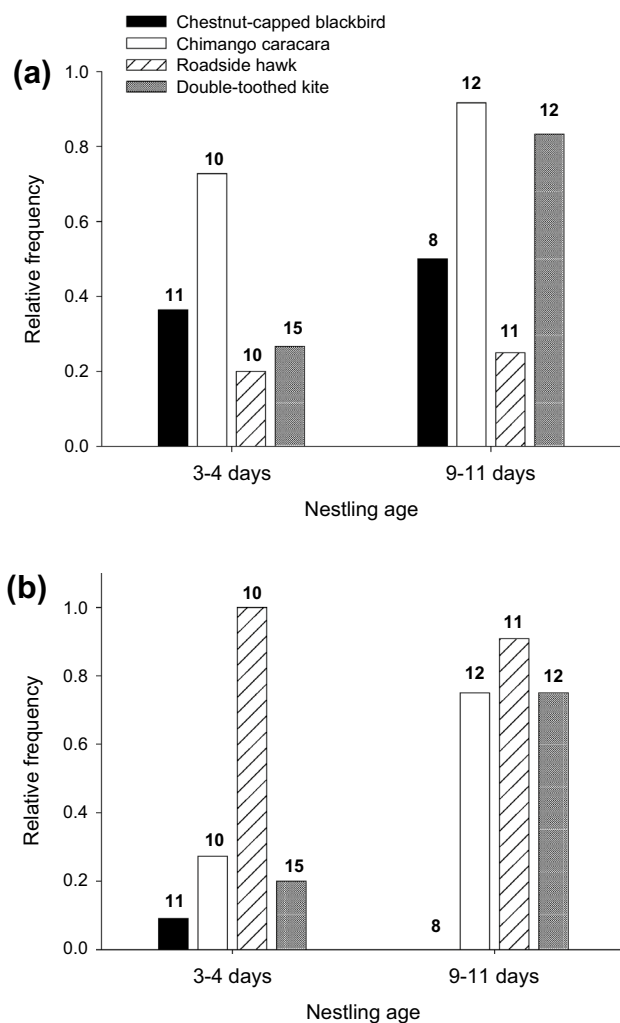
Fig. 4 Relative frequency of alarm calling performed by breeding house wrens during the early and late nestling rearing stage. Nesting southern house wrens performed **a** type I (T I) and **b** type II (T II) alarm calls when exposed to different stuffed specimens. The number above the bars represents the number of experiments in which we recorded alarm call responses from the breeding pairs. A breeding pair can utter neither, one or both alarm call types, so the sum of experiments in which we recorded type I and type II may be lower than, equal to, or higher than the number of experiments performed

trials (76 %), or, when they did, they took a longer time to resume nest activities than when exposed to the chimango caracara. Therefore, house wrens seem to exhibit a threat-sensitive antipredator response, adjusting their behavior to the threat level of the predator.

Contrary to what we observed in the latency to resume parental activities, nest visitation rates were not affected by the presence of the predator dummies once a parent decided to resume parental activities. Whereas the time taken to resume parental activities may reliably reflect the level of risk represented by the dummies, the absence of differences in the nest visitation rates would be the consequence of the

devaluation of these threat levels once the individuals had direct experience with the dummies.

Alarm calling also varied with the predator model presented. When faced with the chimango caracara model, southern house wrens emitted mainly type I alarm calls, whereas when faced with the roadside hawk model, they uttered mainly type II alarm calls (Fig. 4). This difference could correspond to the different functions that calls have (Fasanella and Fernández 2009). It has been suggested that type I alarm calls might be emitted to attract the predator's attention away from the nest, or as a "pursuit-deterrent" signal, informing the predator that it has been detected and encouraging it to depart, although other alternative hypotheses cannot be excluded. The broad frequency band and the relatively long duration of these calls make the caller noticeable, and they can sometimes be accompanied by a close approach of the caller to the threat or overflying behavior. These behaviors can make the caller conspicuous and may imply a serious risk if the threat is a predator of adult birds, as is the case for the roadside hawk (Fernández et al. 2012). In contrast, type II alarm calls are low frequency and narrow bandwidth, making detection of the caller difficult, helping it remain hidden and evasive. These calls have been suggested to be used for intraspecific communication (Fernández et al. 2012), and possibly, uttering type II calls would be used to alert the mate and also the nestlings about the presence of a threat near the nest.

We also found an increase of alarm calling with the nestling age, which has also been observed in previous studies (Fasanella and Fernández 2009; Fernández and Llambías 2013). This increase could imply that these calls are given to silence the nestlings (see Serra and Fernández 2011) or as a response to the increase of the brood value. Specific experiments are necessary to test the effective function of these calls.

Our experiment also provides evidence supporting the hypothesis that house wrens are able to recognize an unknown predator. When faced with the double-toothed kite dummy, nesting house wrens took a longer time to resume parental activities and reduced their nest visits compared with when exposed to the control model. These responses were similar to those recorded when exposed to the chimango caracara model. We propose that this response is the result of a generalization process, facilitated by the similarity between the predator dummies.

Generalization of predator recognition could be based on general characteristics that are shared by the predators. Possible mechanisms involved in such recognition range from a simple cue to a perceptual template that includes several body and signal cues (Barret 2005; Beránková et al. 2014, 2015). The prey can infer the threat associated with an unknown species based on previous experience with known predators (Curio 1975; Hirsch and Bolles 1980; Griffin et al.

Table 2 Comparison of frequency of alarm calls uttered by breeding house wrens when exposed to a control dummy model (chestnut-capped blackbird), to sympatric predator dummy models (chimango caracara or roadside hawk), and to a novel nonsympatric predator (double-toothed kite)

Dummy model	Chestnut-capped blackbird	Chimango caracara	Roadside hawk	Double-toothed kite
Chestnut-capped blackbird	–	2.27	1.72	0.52
Chimango caracara	2.61*	–	3.41**	2.08
Roadside hawk	4.13**	2.83*	–	2.26
Double-toothed kite	2.45*	0.33	3.07*	–

Off-diagonal values represent the z-statistics of the comparison of coefficients derived from the analyses of type I (above) and type II alarm calls (below) according to pairwise post hoc Tukey HSD tests

* $p < 0.05$; ** $p < 0.01$

2001; Ferrari et al. 2007; Ferrari 2009; Chivers and Ferrari 2013). In this way, southern house wrens may respond to characters that the double-toothed kite shares with other known birds of prey, such as body shape, size, contrasting colored and forward-facing eyes, hooked beak, and conspicuous claws (Veselý et al. 2016). However, the response of house wrens to the double-toothed kite differed from that given when exposed to the roadside hawk dummy, presenting more aversion to the latter. These species could represent a similar threat to the wrens, as they are highly generalist in their diet (see references above), and both can prey on small passerines such as wrens. This failure in the specific threat assessment of house wrens appears to indicate that a generalization process is providing a conservative basal response to possible threats and that fine-tuned discrimination comes from direct experience with the predator (Csermely et al. 2006; Carlson et al. 2017b). Shalter (1978) showed that experience of pied flycatchers (*Ficedula hypoleuca*) with a live predator improved the recognition and response to stuffed models of this species. This experience with live predators would favor a perceptual priming process that could facilitate predator recognition (Shalter 1978; Němec et al. 2015).

In addition to using morphological similarity to recognize potential predators, the response of house wrens could be based on body characteristics that may provide additional indirect information about the threat; For example, the response of wrens could be based on the size of the predator species. It has been found that birds can respond differentially to a predator depending on its size (Palleroni et al. 2005; Templeton et al. 2005; Chivers and Ferrari 2013; Beránková et al. 2015). In our experiment, chimango caracaras and double-toothed kites have similar sizes (~30 cm long), whereas roadside hawks are slightly larger (~40 cm). Thus, predator size could be an additional, simple, and quick cue that preys use to adjust their generalized response.

The use of dummy models to evaluate the response of individuals to predators may entail some problems in that

they do not faithfully represent the predator's behavior nor are they likely to exhibit the full range of cues (beyond the visual ones) that may be used by potential prey to recognize them. However, these have been widely used in predator recognition experiments (see Caro 2005 for a review), and it has been observed that, in many cases, they triggered antipredator responses that do not differ from those generated by the presence of a live predator (Shalter 1984; Curio 1993). In our study, responses observed in nesting house wrens when exposed to dummy models were similar to those observed when faced with a live predator (G.J.F., personal observation). Also, our experimental design allowed us to differentiate the response to different predator stuffed models, so we consider that it is a useful and reliable methodology to analyze the house wren responses. The use of stuffed predator models also was adequate as it has been found that birds can respond differentially to dummies built with different materials (see Němec et al. 2015). In their study, Němec et al. found that more reliable and stronger responses were given when exposing birds to natural stuffed or plush-made predator models.

In summary, we found that house wrens show a threat-sensitive predator response, matching their antipredator response to the level of risk represented by the predator. Also, house wrens were able to recognize a nonsympatric predator with similar characteristics to those known by the birds, but fine-tuned discrimination of predator species and adjustment of the level of defense might require an additional learning process. The cues used by southern house wrens to discriminate between raptor species with similar appearance deserve further additional study.

Compliance with Ethical Standards

Ethical Approval All methods used in the present study meet the ethical requirements for science research and comply with the current laws of the country in which they were performed.

Conflict of Interest The authors declare that they have no conflicts of interest.

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