

Sexual differences in risk-taking behaviour of the Southern house wren during the nestling rearing stage

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Abstract When faced with a predator near the nest, breeding birds faced a dilemma: to continue providing parental care to their offspring exposing themselves to risk or to desert the nest for a brief period of time, exposing their offspring to harm due to the suspension of parental brooding and feeding. In this study, we analysed the response of nesting Southern house wrens (*Troglodytes aedon musculus*) to a predator model placed near the nest. The experiment was performed in 56 nests when nestling were 3–4 or 10–12 days old. The model (a plastic decoy of the Great Horned Owl *Bubo virginianus*) was placed at 3 m from the nest. Parent risk-taking was measured as the time elapsed for males and females to resume parental activities during the exposition to the model. We found that males and females delayed parental visits when exposed to the predator model, but females resumed them faster than males, irrespectively of the nesting stage. We also found that males refused to enter to the nest more frequently than females when exposed to the predator model. No effect of breeding experience or nesting stages was noted in the risk taking behaviour of adults. We suggest that sexual differences detected in this species reflect the higher ability of females to cope with the nestling needs and its lower lifetime expectancy.

Keywords Brood value · Harm-to-offspring · Life-history traits · Predation risk · *Troglodytes*

Introduction

Predation of nests and attending adults is one of the main factors affecting life time reproductive success of birds (Sargeant et al. 1984; Slagsvold et al. 1995; Slagsvold and Dale 1996; Newton 1998; Caro 2005; Lima 2009). When detecting a threat close to the nest, parents face the dilemma of whether to ensure offspring's development and survival by providing parental care and defending the nest, or to reduce their own probability of injury or death by postponing parental care until the threat is over (Montgomerie and Weatherhead 1988; Dale et al. 1996).

Several studies have evaluated adult's decision making when faced with a nest predator (reviewed in Caro 2005 and Lima 2009); however, studies dealing with parental response to an adult's predator close to the nest are scarce. The few existing studies show that parents tend to reduce the time spent at the nest (Harris 1980), increase the time to resume parental activity (Michl et al. 2000; Thomson et al. 2011; Schaeff and Mumme 2012), and reduce provisioning rates to nestlings (Scheuerlein and Gwinner 2006; Tilgar et al. 2011). The reduction of parental care when faced with a predator may increase parent's survival probability while compromising offspring development and survival. Hence, there is a trade-off between adult survival and the cost of reducing parental care in terms of offspring fitness (Dale et al. 1996).

The resolution of the dilemma faced by parents should depend on the costs and benefits of risk-taking behaviours, and these may vary both between and within individuals. For example, the risk assumed by parents could vary between sexes if males and females differ in quality or ability to provide parental care (Redondo 1989; Gibson and Moehrensclager 2008). In species where only females can perform incubation and brooding, the costs generated by the suspension of female care during early nesting stages will be more important than those derived from the lack of male parental care (Dale et al.

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1996; Michl et al. 2000). Therefore, it is expected that males should assumed fewer risks than females during nesting stages where eggs or nestlings are dependent on female's care. When nestlings are able to thermoregulate, the costs generated by the suspension of care of both sexes will depend on the ability of the other sex to successfully rear the nestlings alone (Montgomerie and Weatherhead 1988).

Variation in risk-taking by parents could also be consequence of variation in parents and offspring's traits. The benefits of risk-taking behaviour increases with the number, quality and age of the offspring (Andersson et al. 1980; Lazarus and Inglis 1986; Brunton 1990; Clark and Ydenberg 1990; Rytkönen et al. 1990, Clutton-Brock 1991; Winkler 1991; but see Regelmann and Curio 1983; Hakkarainen and Korpimäki 1994; Rytkönen et al. 1995; Hainstock et al. 2010) but decreases with re-nesting potential, and adult survival probability (Montgomerie and Weatherhead 1988; Rytkönen et al. 1993; Ghalambor and Martin 2000). Whereas brood size and offspring' quality increases the current reproductive value of the brood, high probability of re-nesting and high adult survival reduces the actual reproductive value of the brood (Winkler 1987; Montgomerie and Weatherhead 1988; Redondo 1989).

The value of the brood may also be dependent on the individual parental ability and experience (Hainstock et al. 2010). The increase of reproductive success with age or experience is common in birds (Pugesek 1983; Nol and Smith 1987; Newton 1992; Forslund and Pärt 1995; Wiktander et al. 2001; Mauck et al. 2004; Hatch and Westneat 2007). The increment of breeding success with age implies a higher reproductive value of the current brood while aging implies a reduction of their residual reproductive value. Therefore, offspring should be more valuable to experienced or older individuals than to younger ones (Curio 1983; Thornhill 1989). Hence, experienced parents may gain higher benefits from risk-taking behaviours than first-time breeders (Montgomerie and Weatherhead 1988).

In this study, we explore the risk-taking behaviour of males and females of the Southern house wren (*Troglodytes aedon musculus*) during the nestling rearing stage when facing a potential predator of adults. Exposing the adults to a predator close to the nest force them to face an important trade-off between exposing themselves to the risk of being predated and reducing the risk of harm to offspring by resuming parental activities. As costs and benefits may differ between sexes and/or brood value, we specifically tested if risk-taking behaviour differs between sexes, nesting stages and first-time vs. experienced breeders. According to the brood value hypothesis (a) risk-taking behaviour should increase with nestling age for both sexes, and (b) experienced birds should assume higher risks than inexperienced ones. Also, as females have lower adult survival probability than males in this species (Drilling and Thompson 1988; Carro 2012), we expected that (c)

females will assume higher risks than males irrespectively of the nestling rearing stage. Finally, if differences in the ability of each parent to cope with the nestling needs are responsible for differences between sexes in risk-taking behaviour, we predicted that (d) females will assume higher risks than males during early nestling rearing stages, but similar to males when offspring became older and acquired the ability for thermoregulation.

Methods

We studied Southern house wrens (herein SHW) nesting in nest boxes near General Lavalle, Buenos Aires province, Argentina (36°26'S, 56°25'W). The study site was located at a coastal woodland of *Celtis tala*, in a private cattle ranch. SHWs are territorial, socially monogamous and resident all year round (Freed 1987; Llambías and Fernández 2009). SHW engage in extra-pair copulations and 33 % of the broods may contain extra-pair young (LaBarbera et al. 2010). At our study site, wrens are strongly philopatric as none of the adults banded in the population were detected outside the study area during an 8-year study (Carro 2012). Both sexes contribute to nest building but only the female incubates the eggs or brood the young (Brewer 2001). Nestlings are fed by both sexes, although males increase feeding effort as nestling develops (LaBarbera et al. 2012; Llambías et al. 2012). Also, 20–68 % of females attempted a second brood after raise successfully an earlier brood each year. The probability of perform a second brood is dependent on the laying date of the first brood, but it appear to be not related to age or body condition of the nesting female (M. Carro, unpublished data).

All experimental birds nested in wooden nest boxes fixed to trees, 1.5 m above the ground. Boxes were newly constructed from pine and Eucalyptus wood, with dimensions of 30.5 × 16.5 × 12.7 cm and a 27 mm in diameter entrance hole located in the front.

We captured unbanded males within the territory using mist-nests before females started building the nest, while unbanded females were captured inside the box using a wig-wag trap when nestlings were 10–11 days old. Experimental unbanded females were not captured until the experiments ended. Males and females were marked with unique combinations of a numbered aluminum ring and three plastic color bands. Almost all adult individuals of the studied population were colour-banded every year (>90 %). Nestlings were also banded at the nest with a unique numbered aluminum ring when they were 10–12 days old (nestling period lasted between 15 and 19 days; P. Llambías, unpublished data). All unmarked individuals at the onset of the breeding seasons, and those that were marked as nestlings in previous breeding seasons were considered to be recruits into the population, and to have no previous breeding experience (inexperienced

or first-time breeders). Banded individuals that survived among years and were observed breeding were considered to be experienced birds. All individuals were sexed using external morphological characteristics (presence of brood patch and cloacae protuberance) or behaviour (only the male sings and only females incubate the eggs). Once nesting started, we monitored the nests every other day and recorded the date that the first egg was laid, clutch size, brood size and hatching date. We only included in the experiments breeding pairs that were rearing broods of four to five nestlings to reduce variation generated by the differences in brood size. Although brood size in this species varied from one to seven nestlings, the most common brood size is four to five nestlings (mean \pm SE, 4.49 \pm 0.12, $n=93$; P. Llambías, unpublished data).

Experimental design

The experiments were performed during October–January 2005–2007 and 2012. We exposed 56 breeding pairs to plastic great horned owl *Bubo virginianus* models (Dalen Gardeneer 16-Inch Molded Owl #OW6; Dalen Products Inc.) as the model of a predator. This model is often used as bird deterrent artefact and preliminary tests showed that house wrens strongly respond to its presence reducing their nest visits and increasing their latency to resume parental duties compared to other predator and control decoys (see also Fasanella and Fernández 2009). The great horned owl is known to predate upon adult passerines (Bent 1948; Marti 1996; Woodman et al. 2005), and therefore, can be recognized by wrens as a potential adult predator. Furthermore, its morphology is convergent with that of other strigid species also present in the study areas that are also common passerine predators (the short-eared owl, *Asio flammeus*, the striped owl, *Asio clamator* and the barn owl, *Tyto alba*). We also exposed SHW breeding pairs to a stuffed model of a chestnut-capped blackbird (*Chrysomus ruficapillus*) as a control. This species inhabit marshes and open areas of our study site, and constitute a non-threatening species for wrens.

Twelve experiments were performed during 2004, 24 during 2005, 10 during 2007 and the remaining 10 during 2012. We performed experiments only in first broods and avoided testing the same birds in different years. We performed experiments with the predator model at 26 nests when chicks were 3–4 days old (young nestlings or YN) and at 30 nest with nestlings 10–12 days old (old nestlings or ON). Additionally we exposed 13 breeding pairs to the control model (seven during YN and six during ON). No control treatments were performed during 2007 and 2012. Treatments were assigned randomly to each nest but we avoid applying the same stimulus to nests that were less than 50 m from each other in a given year (distance among nests averaged 30 m). To avoid habituation to the models we exposed each pair to the model only once during the nesting cycle.

We performed all experiments in the morning (0600–1000 hours) and video recorded them using a Sony Hi8 video camera (Sony Corp., Tokyo). Video recordings were later analysed in the laboratory. We assumed that adults flying to the nest attract predator attention, increasing their risk of being predated or harmed. To record undisturbed parental activity we filmed nests 1–1.5 h before exposing them to the model (pre-exposure period). After the pre-exposure period we placed the model for 0.5 h (exposure period) on the top of a pole 1.5–1.7 m high, ca. 3 m from the front of the box, facing the nest box entrance.

We evaluated male and female parental responses to the models from video-tapes (no observer was present during the experiment). Male and female visits were identified from video recordings using the colour leg bands of each individual. We measured the risk taken by parents recording the amount of time elapsed from the time the model was placed until an adult resumed feeding (latency; Dale et al. 1996).

Statistical analysis

Initially, we tested if individuals were able to recognize and respond to the aversive stimulus comparing the number of experiments where each parent returned to the nest when exposed to the predator or to the control model. Differences in responses to predator and control models were tested using a generalized linear mixed model with the responses of males and females to the models as the binary response (entry/no entry) and model and sex and the interaction term as explicatory variables. Only experiments performed during 2004 and 2005 (when control experiments were done) were included in this analysis, and year was included as a random factor. For this model, we assumed a binomial distribution of errors and a logit link function. We repeated the test considering only the experiments where nests were exposed to the predator model to test for sexual differences in the probability to resume the parental duties when exposed to the predator model. As before, we used a generalized linear mixed model with binomial errors and a logit link function. The responses of males and females during exposure to the predator model were introduced into the model as a binary response (entry or no entry), whereas the sex of the adult (male/female), breeding experience (inexperienced/experienced) and the interaction term were included into the model as predictors nested into the nesting stage (YN/ON). Nest identity and year were included as random factors. Probability to resume parental activities by one parent was independent of the behaviour of the other parent (Phi correlation test, $\Phi=0.25$, $P>0.05$), and therefore, were not included into the models.

In those nests where at least one adult resumed the parental activities when exposed to the predator model, we compared the parent's latency to return to the nest during the pre-exposition period and the exposition period using a repeated-measure generalized linear model, with latency during the pre-

exposition and exposition periods as the repeated measured, and sex (male/female), year (2004/2005) and nesting stage (YN/ON) and the interaction terms as factors. Latency was squared root transformed to meet requirements of homoscedasticity and normality. Also, we tested if the parents' latency to return to the nest differed when they were exposed to the predator model and when they were exposed to the control model using a generalized linear mixed model with a normal error distribution and an identity link function (latency was previously squared-root transformed). Sex (male/female) and model (predator/control) were included as predictor factors, whereas nest identity and year were included as random factors and brood size as an offset. For this last analysis, we included only experiments performed during 2004–2005.

To test for differences in latency between males and females and among individuals with different breeding experience we only considered the experiments where the nests were exposed to the predator model. We used a generalized linear mixed model with a normal error distribution and an identity link function with the squared-root transformed latency as the response variable, sex (male/female) and breeding experience (inexperienced/experienced) as predictors nested within nesting stage (YN/ON), and nest identity and year as random factors, with brood size as an offset.

Latency to enter the nest when exposed to the models may vary with the time elapsed from the last parent visit during the pre-exposition period. Therefore, prior to test for differences in latency between sexes and breeding experiences, we tested for dependencies among latency and the time elapsed from the last visit before the predator and control model was set and the visitation rate during the pre-exposition period. We did not find any relationship between latency and time elapsed from the last parent's visit or visitation rate during pre-exposition (Spearman rank tests, $P > 0.05$, for sex, breeding experience and nesting stage).

We carried out all statistical analyses in GenStat DE3 (VSN International Ltd.). All P values quoted are two-tailed and differences were considered significant at $P < 0.05$. For each analysis, we used residual and normal probability plots to check model assumptions and we selected a final minimal model by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained (Crawley 1993).

Results

In 66 % of the trials where nests were exposed to the predator model ($n = 37$), one or both members of the breeding pair avoided entering the nest during the 0.5-h exposure period. In 24 nests, only the female resumed parental activities when exposed to the predator model, whereas in 11 nests none individual returned to the nest during the exposure and in only

two nests the male was the only parent that returned to the nest. In the remaining 19 nests, both members of the pair resumed parental activities during the exposure to the predator model. None individual refused to enter the nest following the exposition to the control model in any nesting stage. Statistical models confirm these results. Model type and sex were significant predictors of the parental response (Wald_{1, 81} = 7.95, $P = 0.006$, and Wald_{1, 81} = 8.94, $P = 0.004$, respectively).

When exposed to the predator model, the probability of resume parental care varied between sexes being males more prone to refuse to enter the nest (Wald_{2, 51.3} = 10.56, $P = 0.008$; Fig. 1). Males did not resume parental activities in 65.4 % (17/26) of the trials during the early nesting stage, and in 60 % (18/30) of the trials performed during later nesting stages. In contrast, females exposed to the predator model during early nesting stage refused to enter the nest in 23.1 % (6/26) of the trials, whereas during later nesting stages they refuse enter the nest in 26.07 % (8/30) of the trials. We fail to detect any effect of nestling age or breeding experience in the probability of individuals resuming parental activities when exposed to the predator model (Wald_{1, 41.2} = 0.69, $P = 0.45$ and Wald_{2, 93.1} = 4.43, $P = 0.11$, respectively; Fig. 1).

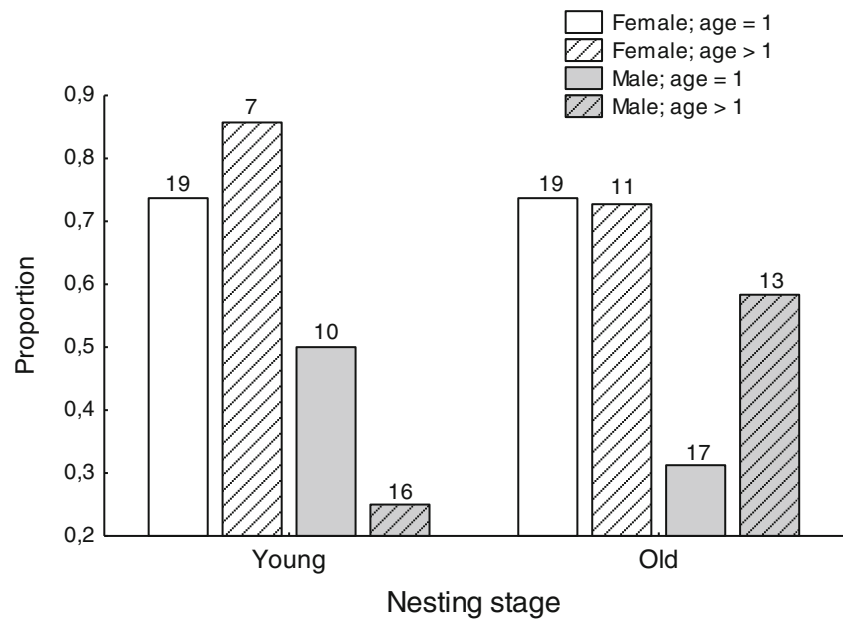
In nests where at least one parent returned to the nest when exposed to the predator model, the time to resume parental activities was significantly longer than the time to return to the nest during the pre-exposure period (mean ± SE, 6.89 ± 0.78 min, and 2.17 ± 0.25 min, for exposure and pre-exposure periods respectively, $n = 42$; $F_{1, 32} = 37.02$, $P < 0.001$). Also, parents' latency to return to the nest was longer when exposed to the predator model than when exposed to the control (mean ± SE, 7.36 ± 0.74 min, $n = 34$, and 2.79 ± 0.65 s, $n = 13$, when exposed to the predator and the control model respectively; Wald_{1, 50.3} = 6.10, $P = 0.02$). However, females resumed their parental activities sooner than males when exposed to both models (Wald_{1, 33.8} = 15.02, $P < 0.01$) and no relationship was found between male and female response (Spearman Rank Correlation, $r = 0.13$, $n = 19$, $P = 0.15$).

In cases where individuals resumed parental care once exposed to the predator model, males' time to resume parental activities was greater than females' (Wald_{2, 22.6} = 20.21, $P < 0.001$; Fig. 2). Experienced birds tended to resume parental activities sooner than inexperienced individuals but this difference was not significant (Wald_{2, 48.6} = 5.01, $P = 0.09$). No effect of nestling stage was detected for the time elapsed to resume parental activities (Wald_{1, 28.2} = 0.21, $P = 0.65$; Fig. 2).

Discussion

Parental risk-taking decisions when faced with a predator are potentially influenced by the reproductive value of offspring, the risk of injury or death that the predator represent to the

Fig. 1 Proportion of inexperienced (first-time breeders) or experienced (with one or more previous breeding attempts) males and females that resumed parental activities when exposed to a predator model during a 0.5-h period (exposure period) when they were rearing 3- to 4-days-old nestlings (*Young*) or 10- to 12-days-old nestlings (*Old*). Numbers upon bars represent the sample size (number of nests)



adult, and the risk of harm to offspring due to the suspension of parental care (Dale et al. 1996). In this study, we found that SHWs respond to a predator of adults close to the nest by increasing the time to resume parental activities. These parental responses, however, varied between sexes. Irrespective of the nestling development, females assumed a higher risk than males, resuming nesting activities more frequently and sooner than males.

Sex differences in risk-taking behaviour and nest defence during parental care have also been observed in other passerine species. Studies on nesting birds with biparental nest defence have found that males assume often more risks during defence than females when faced with a nest predator (Weatherhead 1979; East 1981; Buitron 1983; Breitwisch 1988; Sproat and Ritchison 1993; Regelman and Curio 1996; Hogstad 2005; Gibson and Moehrensclager 2008; Redmond et al. 2009; Kryštofková et al. 2011). This pattern has been attributed mainly to the inability of males to raise young unaided if females die during a nest defense event, particularly during early nesting stages. Therefore, it has been suggested that selection should favor more intense nest defence and risk-taking by males because female's death is certain to result in complete reproductive failure. SHWs show the same parental restrictions with respect to the ability of each sex to raise young successfully. As female perform all incubation and brooding, the breeding attempts will fail if she dies during an encounter with a predator. Only during late nestling stages males can rear nestling to fledge unaided (P. Llambías, unpublished data). Therefore, this explanation cannot account for the greater risk assumed by females observed in this study. Other studies have shown no differences in nest defence intensity between sexes (Tryjanowski and Gólawski 2004;

Fisher and Wiebe 2006; D'Orazio and Neudorf 2008; Tilgar et al. 2011) or, less frequently, that females assume greater risk or spend significantly more time alarm calling than males (Weatherhead 1979; Rytönen et al. 1993).

Alternatively, females may assume greater risks due to the high costs in terms of nestling development and survival associated with the cessation of brooding and feeding of nestlings (Gotlander 1987; Hogstad 2005). However, this hypothesis can only explain the sexual differences in risk-taking behaviour of young nestlings since by day 7 nestlings are able to thermoregulate by themselves (Dunn 1976). As nestlings develop, they become less dependent on maternal care, and parental care cessation of either sex should have similar costs. However, when nestling were 9–11 days old, males were still more risk sensitive than females. Other alternative hypotheses can explain sexual differences in risk-taking behaviour during parental care. Differences in reneating probabilities or confidence of paternity may affect the level of risk that an individual is prone to assume (Montgomerie and Weatherhead 1988; Rytönen et al. 1993). The sex with the lower reneating probability or higher confidence of paternity will take a greater risk due to a greater brood value perception (Barash 1975; Redondo 1989; Clutton-Brock 1991; Møller 1991; Møller and Birkhead 1993; Rytönen et al. 1993; Regelman and Curio 1996; Sheldon et al. 1997; Michl et al. 2000; Hogstad 2005; Rytönen et al. 2007; Seki et al. 2007). Reneating potential when a breeding attempt fails in our population is rather similar for both sexes as mate fidelity is high ($\approx 80\%$; Carro 2012). Hence, the observed higher risk assumed by females does not support the reneating potential hypothesis. In a study on SHWs carried out near our study site, the proportion of extra-pair young within a brood does

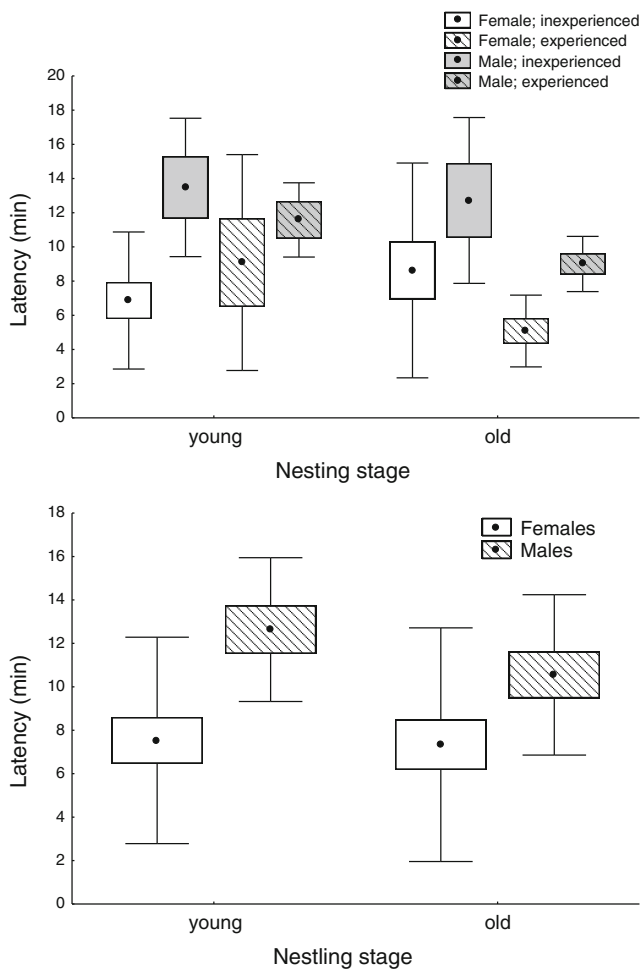


Fig. 2 Latency to return to the nest of inexperienced (first-time breeders) or experienced (with one or more previous breeding attempts) males and females when exposed to a predator model when rearing 3–4-days-old nestlings (*Young*) or 10–12-days-old nestlings (*Old*). Only nests where at least one parent resumed parental activities during the exposure to the predator model were included into the analyses. *Dots* represent median values, *boxes* are the 25–75 % quartile range, and *vertical lines* the total range of values observed

not affect the probability of males providing parental care even though 33 % of nests had at least one extra-pair young (LaBarbera et al. 2010, 2012). Therefore, SHW males may have no reliable cues to assess paternity. If so, differences in risk-taking during parental care may not be a consequence of males' paternity confidence, although an experiment will be necessary to test this hypothesis.

Adult survival may also affect the risk-taking behaviour during nesting (Montgomerie and Weatherhead 1988; Ghalambor and Martin 2000). In most birds, male's adult survival is greater than female's, and thus, males have a higher average residual reproductive success at a given age. Hence, females must assume a higher risk at any nesting stage as reproductive value of a brood will be therefore higher for them

(Andersson et al. 1980; Redondo 1989; Clark and Ydenberg 1990; Dale et al. 1996). At our study site, SWR females have a lower survival probability than males (0.34 vs 0.53 respectively; Cormack–Jolly–Seber models based on marking and resighting of birds in our studied populations during 2005–2011 period; Carro 2012), and, accordingly, we found that females were more prone to resume parental activities and take less time to resume them. Therefore differences in life expectancy and brood value for each sex could at least explain in part the observed differences between sexes.

We failed to detect any effect of breeding experience on risk-taking behaviour in breeding wrens. When faced with a predator model, experienced and inexperienced breeders did not differ in the return frequency or time taken to resume parental activities. Evidence in the scientific literature favoring an age effect on parental risk-taking decisions is rather scarce but the few published studies on passerine species failed to support it (e.g. Curio 1975; Weatherhead 1989; Hatch 1997; but see Redmond et al. 2009). Since mortality probability is independent of age in short-live species, age variation in risk-taking behaviour should not be expected (Montgomerie and Weatherhead 1988). However, other confounding factors (such as physical condition, personality, etc.) can mask the effect of breeding experience on parental decisions in SHWs as suggested by a high variability observed in the response to the predator model in both inexperienced males and females. Specific testing controlling for additional factors can help to elucidate the existence of such an effect.

Our results demonstrate that breeding SHW alter their behaviour during nesting in response to a predation threat. Risk-taking decisions during the feeding of nestlings seem to respond to offspring' needs. The risk of predation may affect not only risk-taking behaviours but parental investment in general as it may affect both adult and offspring life expectancy and the current reproductive value of the brood.

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References

- Andersson M, Wiklund CG, Rundgren H (1980) Parental defence of offspring: a model and an example. *Anim Behav* 28:536–542
- Barash DP (1975) Evolutionary aspects of parental behavior, distraction behavior of the alpine accentor. *Wilson Bull* 87:367–373
- Bent AC (1948) Life histories of North American nuthatches, wrens, thrashers, and their allies. *US Natl Mus Bull* 195:113–141
- Breitwisch R (1988) Sex differences in defence of eggs and nestlings by Northern Mockingbirds, *Mimus polyglottos*. *Anim Behav* 36:62–72
- Brewer D (2001) Wrens, Dippers and Thrashers. Yale University Press, New Haven
- Brunton DH (1990) The effects of nesting stage, sex, and type of predator on parental defense by killdeer (*Charadrius vociferous*): testing models of avian predator defense. *Behav Ecol Sociobiol* 26:181–190
- Buitron D (1983) Variability in the responses of blackbilled magpies to natural predators. *Behaviour* 87:209–236
- Caro T (2005) Antipredator defences in birds and mammals. University of Chicago Press, Chicago
- Carro ME (2012) Dispersión natal y reproductiva de la ratona común *Troglodytes musculus*. PhD Thesis, Universidad de Buenos Aires
- Clark CW, Ydenberg RC (1990) The risks of parenthood. I. General theory and applications. *Evol Ecol* 4:21–34
- Clutton-Brook TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Crawley M (1993) Glim for ecologists. Blackwell Scientific Publications, Oxford
- Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. *Anim Behav* 23:1–115
- Curio E (1983) Why do young birds reproduce less well? *Ibis* 125:400–404
- D’Orazio KA, Neudorf DLH (2008) Nest defense by Carolina Wrens. *Wilson J Ornithol* 120:467–472
- Dale S, Gustavsen R, Slagsvold T (1996) Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. *Behav Ecol Sociobiol* 39:31–41
- Drilling NE, Thompson CF (1988) Natal and breeding dispersal in house wrens (*Troglodytes aedon*). *Auk* 105:480–491
- Dunn EH (1976) The relationship between brood size and age of effective homeothermy in nestling house wrens. *Wilson Bull* 88:478–482
- East M (1981) Alarm calling and parental investment in the robin *Erithacus rubecula*. *Ibis* 123:223–230
- Fasanella M, Fernández GJ (2009) Alarm calls of the Southern house wren, *Troglodytes musculus*: variation with nesting stage and predator model. *J Ornithol* 150:853–863
- Fisher RJ, Wiebe KL (2006) Investment in nest defense by Northern Flickers: effects of age and sex. *Wilson J Ornithol* 118:452–460
- Forslund P, Pärt T (1995) Age and reproduction in birds—hypotheses and tests. *Trends Ecol Evol* 10:374–378
- Freed LA (1987) The long-term pair bond of tropical house wrens: advantage or constrain? *Am Nat* 130:507–525
- Ghalambor CK, Martin TE (2000) Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Anim Behav* 60:263–267
- Gibson KW, Moehrenschrager A (2008) A sex difference in the behavioural response of nesting mountain bluebirds (*Sialia currucoides*) to a mounted predator. *J Ethol* 26:185–189
- Gotlander K (1987) Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scand* 18:269–276
- Hainstock MH, Smith MC, Carr J, Shutler D (2010) Parental investment and brood value in tree swallows, *Tachycineta bicolor*. *Behaviour* 147:441–464
- Hakkarainen H, Korpimäki E (1994) Nest defence of Tengmalm’s owls reflects offspring survival prospects under fluctuating food conditions. *Anim Behav* 48:843–849
- Harris MP (1980) Breeding performance of puffins (*Fraterecula arctica*) in relation to nest density, laying date and year. *Ibis* 122:193–209
- Hatch MI (1997) Variation in Song Sparrow nest defense: individual consistency and relationship to nest success. *Condor* 99:282–289
- Hatch MI, Westneat DF (2007) Age-related patterns of reproductive success in house sparrows *Passer domesticus*. *J Avian Biol* 38:603–611
- Hogstad O (2005) Sex-differences in nest defence in Fieldfares *Turdus pilaris* in relation to their size and physical condition. *Ibis* 147:375–380
- Kryštofková M, Haas M, Exnerová A (2011) Nest defense in blackbirds *Turdus merula*: effect of predator distance and parental sex. *Acta Ornithol* 46:55–63
- LaBarbera K, Llambías PE, Cramer ERA, Schaming TD, Lovette IJ (2010) Synchrony does not explain extra-pair paternity rate variation in northern or southern house wrens. *Behav Ecol* 21:773–780
- LaBarbera K, Lovette IJ, Llambías PE (2012) Mating opportunities, paternity, and sexual conflict: parental care in northern and southern house wrens. *Behav Ecol Sociobiol* 66:253–260
- Lazarus J, Inglis IR (1986) Shared and unshared parental investment, parent-offspring conflict, and brood size. *Anim Behav* 34:1791–1804
- Lima SL (2009) Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biol Review* 84:485–513
- Llambías PE, Fernández GJ (2009) Effects of nestboxes on the breeding biology of southern house wrens *Troglodytes aedon bonariae* in the southern temperate zone. *Ibis* 151:113–121
- Llambías PE, LaBarbera K, Astié AA (2012) Similar patterns of parental provisioning in a monogamous and a polygynous population of the house wren. *Condor* 114:629–638
- Marti CD (1996) Diet and trophic characteristics of great horned owls in Southwestern Idaho. *J Field Ornithol* 67:499–506
- Mauck RA, Huntington CE, Grubb TC (2004) Age-specific reproductive success: evidence for the selection hypothesis. *Evolution* 58:880–885
- Michl G, Török J, Garamszegi LZ, Tóth L (2000) Sex-dependent risk taking in the collared flycatcher, *Ficedula albicollis*, when exposed to a predator at the nestling stage. *Anim Behav* 59:623–628
- Møller AP (1991) Defence of offspring by male swallows, *Hirundo rustica*, in relation to participation in extra-pair copulations by their mates. *Anim Behav* 42:261–267
- Møller AP, Birkhead TR (1993) Certainty of paternity covaries with paternal care in birds. *Behav Ecol Sociobiol* 33:261–268
- Montgomerie RD, Weatherhead PJ (1988) Risk and rewards of nest defence by parent birds. *Quar Rev Biol* 63:167–187
- Newton I (1992) Synthesis. In: Newton I (ed) Lifetime reproduction in birds. Academic Press, New York
- Newton I (1998) Population limitation in birds. Academic Press, London
- Nol E, Smith JNM (1987) Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. *J Anim Ecol* 56:301–313
- Pugesek BH (1983) The relationship between parental age and reproductive effort in the California Gull (*Larus californicus*). *Behav Ecol Sociobiol* 13:161–171
- Redmond LJ, Murphy MT, Dolan AC, Sexton K (2009) Parental investment theory and nest defense by Eastern Kingbirds. *Wilson J Ornithol* 121:1–11
- Redondo T (1989) Avian nest defense: theoretical models and evidence. *Behaviour* 111:161–195
- Regelmann K, Curio E (1983) Determinants of brood defence in the great tit *Parus major* L. *Behav Ecol Sociobiol* 13:131–145

- Regelmann K, Curio E (1996) Why do great tit (*Parus major*) males defend their brood more than females do? *Anim Behav* 34:1206–1214
- Rytkönen S, Koivula K, Orell M (1990) Temporal increase in nest defence intensity of the willow tit (*Parus montanus*): parental investment or methodology methodological artifact? *Behav Ecol Sociobiol* 27:283–286
- Rytkönen S, Orell M, Koviula K (1993) Sex-role reversal in Willow Tit nest defence. *Behav Ecol Sociobiol* 33:275–282
- Rytkönen S, Orell M, Koivula K, Soppela M (1995) Correlation between two components of parental investment: nest defense intensity and nestling provisioning effort of willow tits. *Oecologia* 104:386–393
- Rytkönen S, Kvist L, Mikkonen R, Orell M (2007) Intensity of nest defence is not related to degree of paternity in the willow tit *Parus montanus*. *J Avian Biol* 38:273–277
- Sargeant AB, Allen SH, Eberhardt RT (1984) Red fox predation on breeding ducks in midcontinent North America. *Wildl Monog* 89: 1–41
- Schaefer KM, Mumme RL (2012) Predator vocalizations alter parental return time at nests of the Hooded Warbler. *Condor* 114:840–845
- Scheuerlein A, Gwinner E (2006) Reduced nestling growth of East African Stonechats *Saxicola torquata axillaris* in the presence of a predator. *Ibis* 148:468–476
- Seki M, Wakano JY, Ihara Y (2007) A theoretical study on the evolution of male parental care and female multiple mating: Effects of female mate choice and male care bias. *J Theor Biol* 247:281–296
- Sheldon BC, Räsänen K, Dias PC (1997) Certainty of paternity and paternal effort in the collared flycatcher. *Behav Ecol* 8:421–428
- Slagsvold T, Dale S (1996) Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. *Ecology* 77:461–471
- Slagsvold T, Dale S, Kruszewicz A (1995) Predation favours cryptic coloration in breeding male pied flycatchers. *Anim Behav* 50: 1109–1121
- Sproat TM, Ritchison G (1993) The nest defense behavior of Eastern Screech-owls: effects of nest stage, sex, nest type and predator location. *Condor* 95:88–296
- Thomson RL, Forsman JT, Mönkkönen M (2011) Risk taking in natural predation risk gradients: support for risk allocation from breeding pied flycatchers. *Anim Behav* 82:1443–1447
- Thornhill R (1989) Nest defense by Red Jungle Fowl (*Gallus gallus spadiceus*) hens: the roles of reneating potential, parental experience and brood reproductive value. *Ethology* 83:31–42
- Tilgar V, Moks K, Saag P (2011) Predator-induced stress changes parental feeding behavior in pied flycatchers. *Behav Ecol* 22:23–28
- Tryjanowski P, Gólawski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. *J Ethol* 22:13–16
- Weatherhead PJ (1979) Do savannah sparrows commit the Concorde Fallacy? *Behav Ecol Sociobiol* 5:373–381
- Weatherhead PJ (1989) Nest defence by Song Sparrows: methodological and life history considerations. *Behav Ecol Sociobiol* 25:129–136
- Wiktander U, Olsson O, Nilsson SG (2001) Age and reproduction in lesser spotted woodpeckers (*Dendrocopos minor*). *Auk* 118:624–635
- Winkler DW (1987) General model for parental care. *Am Nat* 130:526–543
- Winkler DW (1991) Parental investment decision rules in tree swallows: parental defense, abandonment, and the so called Concorde Fallacy. *Behav Ecol* 2:133–142
- Woodman N, Dove CJ, Peurach SC (2005) A curious pellet from a Great Horned Owl (*Bubo virginianus*). *Northeast Nat* 12:127–132