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Parental risk-taking behaviour and nest defence during the nestling rearing stage in Northern House Wrens *Troglodytes aedon*

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Abstract. Risk-taking behaviour of short lived nesting birds is often explained in relation to the reproductive value of offspring (the reproductive value hypothesis) and the harm that the absence of parental care can cause to nestlings (risk of harm-to-offspring hypothesis). The reproductive value hypothesis predicts that the risk assumed by adults should increases with nestling age, whereas the risk of harm-to-offspring hypothesis predicts the opposite pattern. We assessed the risk-taking behaviour of nesting males and females Northern House Wrens, *Troglodytes aedon*, faced with a predation threat (plastic owl model) when rearing 3–4 and 10–12 days old nestlings. We used the time elapsed until parents first entered the nest-box as a measure of risk-taking behaviour and alarm calling rate as a proxy of nest defence. Females resumed sooner parental activities when exposed to the model when nestlings were young, supporting the risk of harm-to-offspring hypothesis. In contrast, the time lasted to resume parental duties by males did not differ between nestling ages. Alarm calling rate increased with the nestling stage, as predicted by the reproductive value hypothesis. We suggest that nesting House Wrens responded to both nestling requirements and to the reproductive value of the brood, assuming greater risks when nestlings are more vulnerable and a more intense nest defence when nestlings are older.

Key words: predation risk, nest defence, risk taking, nestling vulnerability, brood value

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INTRODUCTION

Predation risk for parents and offspring is one of the main factors that affect reproductive success and parental investment decisions (Montgomerie & Weatherhead 1988, Lima & Dill 1990, Lima 2009, Jaatinen et al. 2011). Parental investment decisions are assumed to be based upon the trade-off between the benefits of investing in the current reproductive event and the costs of reduction of future reproductive success (Trivers 1972, Clutton-Brock 1991, Roff 1992).

Variation in risk-taking behaviour and nest defence when parents are faced with a threat at the nest has been considered an effective indicator of parental investment strategies (e.g., Weatherhead 1989, Dale et al. 1996, Onnebrink & Curio 1991, Forbes et al. 1994, Ghalambor & Martin 2000). When nesting birds are exposed to a predator, individuals face a dilemma, whether to protect the brood and continue feeding and brooding the nestlings, exposing themselves to harm or predation, or to hide and increase their own probability of survival and future reproduction (Dale et al. 1996, Listřen et al. 2000, Michl et al. 2000, Ghalambor & Martin 2001).

Parental investment theory (PI) proposes that the risk-taking decision must be based upon a trade-off between the marginal benefits obtained from assumed risks when protecting the offspring and the costs in terms of fitness loss if such actions were not taken. One of PI predictions is that individuals should invest more heavily in nest defence and assume greater risks when the brood's reproductive value is higher (the "reproductive or offspring value hypothesis"; Trivers 1972, Barash 1975, Montgomerie & Weatherhead 1988, Redondo 1989). The reproductive value of the brood increases with the number and age of the offspring, hence parents should assume greater risks and defend their offspring more intensively when nestlings are older and/or the brood is larger (Anderson et al. 1980, Lazarus & Inglis 1986, Brunton 1990, Clark & Ydenberg 1990, Rytkönen et al. 1990, Winkler 1991, Dale et al. 1996, Tryjanowski & Golawski 2004). In birds, a number of studies have found that nest defence behaviours such as alarm calling, mobbing and attacks to a predator increases with the reproductive value of the brood providing support to this hypothesis (reviewed by Montgomerie & Weatherhead 1988, Wiklund 1990, Clutton-Brock 1991, Caro 2005). To explain a reversed pattern of nest defence and risk-taking observed in several bird species, Dale et al. (1996) proposed the "risk of harm-to-offspring" hypothesis which proposes that parental risk taking is related to the harm that offspring will suffer during periods without parental care, when eggs are not being incubated or nestlings are not brooded or fed (Montgomerie & Weatherhead 1988, Dale et al. 1996, Listřen et al. 2000). Under this hypothesis, parents should assume higher risks and invest heavier in nest defence when young are more vulnerable to parental care deprivation (e.g. during the nestling's ectothermic phase).

Benefits derived from continue parental care in presence of a threat may vary between males and females if they differ in ability or quality to provide that care (Redondo 1989, Gibson & Moehrenschlager 2008). For example, in species where females perform all incubation and brooding during early nestling rearing stages, the costs generated by the cessation of female care during these stages will be more important than those derived from the lack of male parental care (Dale et al. 1996, Michl et al. 2000). Therefore, it is expected that in these cases females should assume higher risk than males, and resume parental duties sooner. Sexes also could differ in their perception of the brood value according to ecological and life history trait differences. For example, differences between sexes in renesting probability, adult survival, or parenthood certainty should affect the brood value perception, and therefore, affect the risk-taking behaviour during parental care (Barash 1975, Andersson et al. 1980, Redondo 1989, Clark & Ydenberg 1990, Rytkönen et al. 1990, Regelmann & Curio 1996, Michl et al. 2000, Högstad 2005, Klvaňová et al. 2011, Polak 2013).

In this study, we tested simultaneously the harm-to-offspring and brood-value hypotheses in the Northern House Wren, *Troglodytes aedon aedon*. Although predictions of the reproductive-value and the harm-to-offspring hypotheses are opposed, they may not be mutually exclusive (Dale et al. 1996) and few studies have tested these hypotheses simultaneously (but see Michl et al. 2000). We analyzed the parental risk-taking behaviour and nest defence of the Northern House Wren, during the nestling rearing stage exposing breeding pairs to a model of a predator when rearing young (3–4 days old) or old nestlings (10–12 days old). We assessed males and females responses and analyzed if parental response differ between sexes. If parents respond according to the reproductive value of offspring, we expected them to perform greater nest defence when nestlings are older. However, if parental decision responds to the risk of harm-to-offspring, differences between sexes in the response to the threatening model are expected as only females can perform the brooding of chicks. Hence, females should accept a higher risk than males during the period when nestlings have a limited capability of thermoregulation (Dunn 1976).

MATERIALS AND METHODS

Study species

The Northern House Wren is a small (approximately 10 g) sexually monomorphic, migratory passerine that is distributed across most of North America (Johnson 1998). They breed in natural cavities, holes excavated by other birds and nest-boxes (Kendeigh 1941, Johnson 1998). Early in the breeding season the males arrive to the breeding grounds and settle to defend a territory. Nests are built by both sexes, but only the female complete the nest cup with lining. Clutch size varies from four to eight eggs and the incubation period lasts approximately 13 days (Johnson 1998, Llambías 2009). Both parents feed nestlings, but eggs are incubated and nestlings are brooded exclusively by the female. Nestlings fledge after 15–17 days (Johnson 1998). Wrens nesting in nest boxes have usually lower nest predation rates than those nesting in tree cavities (Johnson & Kermott 1994, Purcell et al. 1997). In our study area (see below) about 87% of nests were successful. Main nest predators are squirrels (*Tamasciurus* spp., *Sciurus* spp.), rats (*Rattus* spp.), mice (*Peromyscus* spp.), and woodpeckers (*Melanerphes* spp.). Opossums (*Didelphis* spp.), raccoons (*Procyon lotor*), weasels (*Mustela frenata*) and snakes (genus *Thamnophis*, *Lampropeltis*, and *Elaphe*) have also been reported to prey upon eggs or nestlings (Finch 1990, Johnson 1998). Domestic cats (*Felis catus*), foxes (genus *Vulpes*) and owls (*Bubo virginianus*, *Megascops* spp.) are known as predators of both adults and young outside the nest cavity (Bent 1948, Johnson 1998).

Study site and field procedures

We studied Northern House Wrens breeding in nest boxes located at mixed deciduous patches of forests at Cornell experimental ponds near Ithaca, New York State, USA (42°28′N, 76°29′W) during May–August 2004–2005.

All experimental birds nested in wooden nest-boxes fixed to greased poles, 1.5 m above the ground. Boxes measured 30.5×16.5×12.7 cm, and the diameter of the entrance hole was 38 mm. We captured and banded males at the onset of the breeding season when they started defending territories. Unbanded females were captured inside the boxes after we performed the experiments. In all experiments at least one adult was previously banded so we could identify male and female. We monitored nests every other day and recorded the first egg laying date, clutch size, brood size and hatching date. We only included monogamous pairs in the experiments.

Experimental design

We exposed 32 House Wren 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. These models are often used as bird deterrent artefacts, and, when exposed to this model, House Wrens respond reducing parental nest visits and performing active nest defence by calling (PEL, unpubl. data). Due to the model size and that the Great Horned Owl could predate upon adult wrens (Bent 1948), we assumed that the model represent a higher threat for adults than for nest content.

We performed experiments only in first broods and avoided testing the same birds in different years. Brood size in these nests varied from 4 to 8 nestlings (median = 6 nestlings). We performed the experiment when chicks were unable to thermoregulate (3–4 days old, young nestlings; n = 15 nests), or next to fledge (10–12 days old, old nestlings; n = 17 nests). According to Dunn (1976), chicks can reach physiological endothermy when they are 6–7 days old. To avoid bird habituation to the model, we exposed each breeding pair to the model only once during the nesting cycle.

We performed all experiments in the morning (06.00–11.00 h) and video recorded them using a Sony Hi8 video camera (Sony Corp.). Video recordings were later analysed in the laboratory. We assumed that adults flying to the nest attract predator attention, increasing their own predation risk or assuming a higher risk of harm. We placed the video camera about 8–10 m from the nests focusing on nest entrance to record parent activity. Cameras were camouflaged and placed 1–1.5 h before the start of filming to allow the breeding pair to habituate to its presence. After this period, we filmed the nest for 1 hr previous to placing the predator model (Pre-exposure period) to control for parental nest attention without any stimulus. After this 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 and filmed the parental response. When we were placing the model, adults were flashed from the nest box (no bird remained inside the nest box when we started the Exposure period). During these periods (Pre-exposure and Exposure) none observer was present except when we switched the camera on and during the placement of the model.

We evaluated parental responses to the model from video-tapes. 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, Ghalambor & Martin 2000). The parents' risk-taking and the return time are assumed to be inversely related. We also measured latency to resume the activity at the nest during the pre-exposure period to control for variation in parental nest activity and for any undesirable effects of researcher activity when the model was set.

We quantified the nest defence performed by nesting wrens measuring the time that wrens spent calling when we placed the model in front of the nest. Males and females produced vocalizations in response to the presence of a threat near the nest (Johnson 1998). When the threat involve the presence of a small predators (such as snakes and rodents), males and females usually chase and sometimes strike them with feet and bill (Johnson & Albrecht 1993), but rarely attack larger predators (although occasionally strike humans at nest; Johnson 1998).

We identified two different calls during the experiments: a harsh, raspy scolding call (Fig. 1a), and a loud chatter call (Fig. 1b). We measured the time that nesting wrens uttered these call during

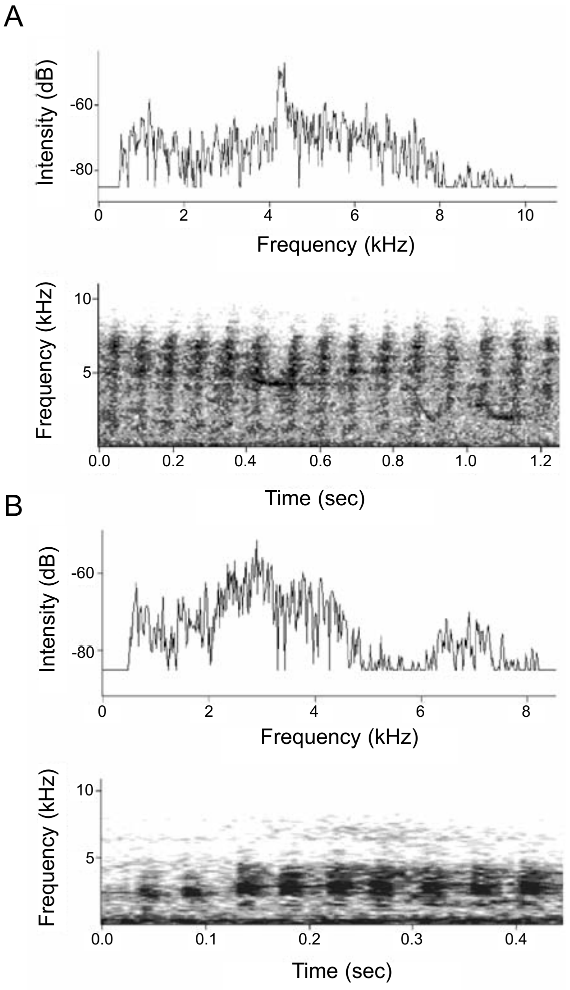

Fig. 1. Power spectrum (above) and spectrograms (below) of House Wren calls recorded during experimental trials. A) Scolding calls; B) Chatter calls.

the first ten minutes after the exposition to the model using Etholog 2.2 (Ottoni 2000). Due to the high environmental noise in the recordings, we were only able to analyse alarm calling in ten experiments carried out during the early nestling rearing stage and ten experiments during the late nestling stage.

Statistical analysis

We examined the risk-taking behaviour of House Wren breeding pairs during the nestling period analysing the time adults took to resume parental activities when exposed to the model and the number of essays that any parent refused to enter the nest during the exposition to the model. The number of individuals that refused to enter the nest during exposure to the predator model was analysed treating it as a binary response (entry or no entry) in a generalized linear model (GLM) with binomial errors and a logit link function, brood size as a continuous predictor, and nesting stage (young and old nestlings), and their two-way interaction as factors. We also used Fisher exact tests to analyse sexual differences in the behaviour of refuse to enter the nest.

We used a generalized linear mixed model (GLMM) to compare parental behaviour during pre-exposure and exposure periods, including latency to enter the nest as the response variable, brood size as a continuous predictor, the experimental period (pre-exposure or exposure) and nesting stage (young or old nestlings) and the two- and three-way interactions as predictors, and nest as a random variable to control for the lack of independency between these periods. We assumed a model with normal errors and an identity link function for latency. We repeated this analysis separately for males and females to assess the responses of each sex to the aversive stimulus, assuming a model with gamma distribution errors and a reciprocal link function for latency. To compare male and female responses to the model, we performed a GLMM with latency to entry to the nest when exposed to the predator model as the response variable, and brood size, sex, nesting stage and the interaction terms as predictors in a model, assuming a gamma distribution of the errors and a reciprocal link function.

We used residual and normal probability plots to check model assumptions in all analyses. We selected the final models by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained. When interaction between factors was significant, we performed a GLM to assess individual effects. We assessed the significance of factors in the models using the deviance ratio (Dr) or variance ratio (Vr) for the variable or interaction terms (Crawley 1993).

We also performed a GLM to compare the total time that parents spend alarm calling between nestling stages, assuming a gamma error distribution and a reciprocal link function. We took the the total time the adults spend alarm calling as the response variable, and we used brood size as a continuous predictor, and nesting stage (young and old nestlings), and their two-way interactions as factors in the model. We used residual and normal probability plots to check model assumptions. We selected a final model by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained. We assessed the significance of factors in the models using the change in deviance for the variable or interaction terms (Crawley 1993).

We carried out statistical analyses in GenStat DE3 (VSN International Ltd.). All p-values quoted are two-tailed and differences were considered significant at $p < 0.05$.

RESULTS

Risk taking

Five breeding pairs (13.5%) refused to enter the nest when exposed to the predator model. The probability of adults entering the nest was not explained by brood size, nesting stage or the interaction term (Dr = 0.08, df = 3,31, p = 0.97). However, females tended to assume greater risk than males as they entered the nest on 87% of experiments with young nestlings and on 81% with old nestlings, whereas males resumed parental activities when exposed to the model on 60% and 28% of times respectively (Fisher exact test, p = 0.1 and p = 0.005, for young and old nestlings respectively). Neither, brood size or nesting stage, nor the interaction terms explained the probability to refused to enter the nest when exposed to the model for either males or females (Dr = 0.87, df = 3,27, p = 0.46; and Dr = 0.08, df = 3,27, p = 0.97; respectively).

Wrens resumed later parental duties during the exposure to the model than during the pre-exposure period (Wald = 40.84, df = 1,31, $p < 0.001$; Fig. 2a). Also, latencies of parents to enter the nest in the different nestling stages varied according the trial period (Wald = 4.25, df = 1,31.1, p = 0.04, for the interaction term). During the pre-exposure period wrens had similar latencies when they were rearing young and old nestlings (Vr = 1.14, df = 3,30, p = 0.35; Fig. 2a). However, when exposed to the predator model, breeding birds resumed parental activities sooner when rearing young nestlings than when rearing old nestlings (Vr = 6.32, df = 1,25, p = 0.02; Fig. 2a). We did not detect any effect of brood size on the latency to resume parental activities, both during the pre-exposure and exposure periods ($p > 0.5$).

Both, males and females returned later to the nest when exposed to the predator model (males — Wald = 8.87, df = 1,34, p = 0.005; females — Wald = 30.33, df = 1,46, $p < 0.001$). No differences in latency to resume parental duties between nesting stages was detected for males (Wald = 0.73, df = 1,34, p = 0.4), but females tended to return to the nest sooner at early nesting stages than at a later stage (Wald = 9.16, df = 1,46, $p < 0.001$; Fig. 2b). No effect of brood size was detected for both male and female latency to return to the nest (males — Wald = 0.16, df = 1,34, p = 0.70; females — Wald = 0.17, df = 1,41, p = 0.68). Besides male behaviour did not differ between nestling stages, we failed to find differences in latency between sexes (Wald = 1.33, df = 1,21.5, p = 0.26), probably due to the low number of cases where male return to the nest when they were rearing old nestlings.

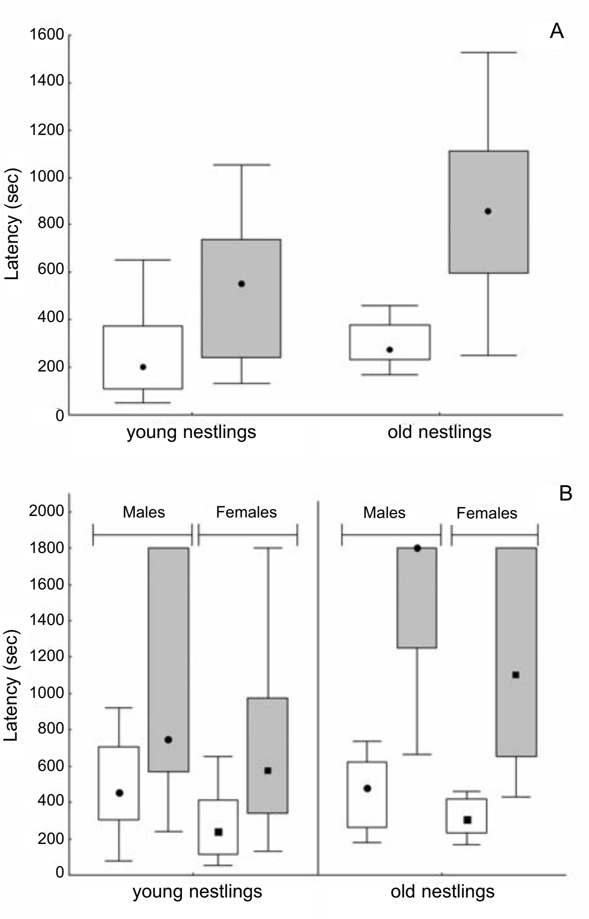

Fig. 2. Variation of latency in entering the nest of Northern House Wrens during the rearing of young (3–4 days old) and old (10–12 days old) nestlings, when exposed to a predator model. A) Overall latency (males + females); B) male and female latency to enter the nest. Blank bars — latency to enter the nest in the Pre-exposition period (period before the exposition to the predator model), grey bars — the latency to enter to the nest when breeding birds were exposed to the model (treatment). In B) we included the maximum time when birds did not return to the nest (1800 sec). Dots and squares represent median values, boxes are the 25–75% quartile range, and vertical lines the total range of values observed.

Nest defence

Similarly to the risk-taking analysis, only nesting stage explained variation observed in adult uttering scolding and chatter calls (Vr = 6.36, df = 1,19, p = 0.02, and Vr = 5.61, df = 1,19, p = 0.03), but in this case time that parents spent calling was higher when nestlings were older (Fig. 3). Responses of males and females could not be distinguished because the camera was focusing to the nest entrance, so we cannot assess sexual differences in nest defence.

DISCUSSION

Parental investment theory predicts that, when faced with a potential risk, the response of individuals depends on the difference between the marginal gain of parental care and the cost of the assumed risk (Trivers 1972, Montgomerie & Weatherhead 1988, Clutton-Brock 1991). While the reproductive value hypothesis predicts that risk-taking behaviours should increase with nestling age, the risk of harm-to-offspring hypothesis predicts the opposite pattern due to nestlings' dependence on parental care at an early age (Dale et al. 1996). In this study, we found that Northern House Wren females took a greater risk when nestlings were more vulnerable to the lack of parental care, supporting the risk of harm-to-offspring hypothesis. When threatened by a model predator, females feeding 3–4 days nestlings reduced the latency to enter the nest and resumed parental activities faster than those feeding 10–12 days old nestling. During the early nestling stage, chicks can be negatively affected from the lack of parental care due to the rapid loss of body heat, since effective endothermy develops later in the nestling stage (Dawson & Evans 1957, Dunn 1976). In the Northern House Wren, physiological endothermy is not reached until nestlings are at least 6–7 days old (Kendeigh & Baldwin 1928, Dunn 1976). The reduction in body temperature of young nestlings likely leads to reduction in enzymatic activity which deters nestlings from digesting food and using body reserves (Gill 2007).

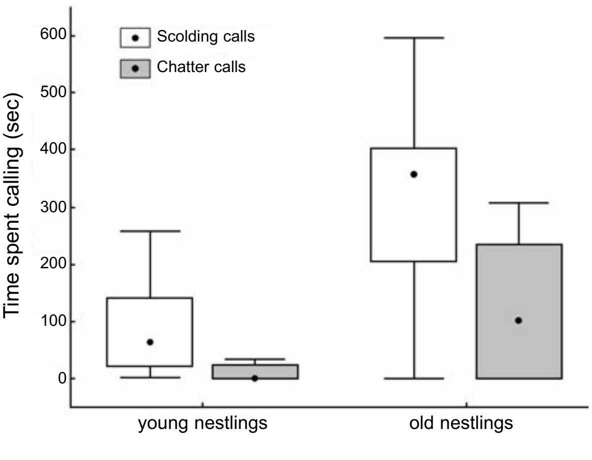

Fig. 3. Variation of scolding and chatter calls of nesting Northern House Wrens uttered during the rearing of young (3–4 days old) and old (10–12 days old) nestlings, when exposed to a predator model. Dots represent median values, boxes are the 25–75% quartile range, and vertical lines the total range of values observed.

The observed sexual differences in risk-taking behaviour could be explained by considering the different parental care roles that males and females have in this species. In House Wrens, egg and nestling survival depends on female incubating and brooding behaviour, so females could be expected to assume higher risks during early nesting stages than males. Indeed, females responded returning to the nest in a higher number of experiments than males. The response of females appears, therefore, to be constrained by the vulnerability of offspring. But does the marginal value obtained from protecting offspring while exposing themselves to risk compensates the potential reduction in future reproductive success? In this population, male House Wrens have a higher survival probability than females (0.48 vs. 0.33; Llambías 2009), and therefore, a nesting attempt should have a lower current reproductive value for males than for females (Montgomerie & Weatherhead 1988, Clark 1994). Life history theory predicts that longer-lived individuals will take fewer risks when exposed to a predation risk than shorter-lived ones (Anderson et al. 1980, Clark & Ydenberg 1990, Clutton-Brock 1991). However, the small difference in survival probability we observed (≈ 15%) appears not to be enough to explain the sexual differences we observed. Other explanations to sexual differences in risk-taking are related to confidence of paternity and re-mating opportunity (Regelmann & Curio 1983, Redondo 1989, Michl et al. 2000, Högstad 2005). In species where adults could increase their reproductive success through additional mates, the current reproductive value of the brood for the polygamous sex would be reduced relative to their mates. Indeed, in our study population, 33% of the broods and 16% of the young are extra-pair (LaBarbera et al. 2010), reducing the benefits of risk-taking behaviours for males. Furthermore, males make fewer trips to the nests with food when more local females are fertile (LaBarbera et al. 2012). Therefore, sexual differences in the risk-taking behaviour pattern that we observed could be explained at least partially by the differences in reproductive value of the brood for males and females.

Breeding individuals also increased the alarm calling with nestling age, such as is expected by the offspring reproductive value hypothesis. Therefore, House Wrens faced with a predator appear to make a greater nest defence investment when rearing old nestlings but assuming fewer risks. In several studies, alarm calls are considered effective nest defence behaviours, as they distract or dissuade predators (Anderson et al. 1980, Curio & Regelmann 1985, Westnead 1989, Kryštofková et al. 2011) or attract neighbours to cooperatively mob the predator (Colombelli-Négrel et al. 2010, Krama et al. 2012). However, other studies considered that alarm calling could be oriented to warn mates or nestlings (Greig-Smith 1980, Kleindorfer et al. 1996, Platzen & Magrath 2004, Madden et al. 2005, Suzuki 2011). Under this scheme, alarm calls may not be seen as a nest defence behaviour but a communication system among close relatives which purpose is to reduce the conspicuousness of the nest by reducing nestling begging intensity and activity (Onnebrick & Curio 1991). Indeed, in the Southern House Wren (*T. a. musculus*), it was found that 9–11 days old nestlings responded to adult alarm calls reducing their vocalizations and activity at the nest (Serra & Fernández 2011). Hence, adult response to a predator may be independent of the offspring reproductive value, but related to the increased conspicuity and responsiveness of nestlings with age. However, if this was the solely purpose of alarm calling, we would expect that this behaviour should not be present when nestling are 2–3 days old, when begging and movement are highly reduced. Furthermore, at this stage, alarm calling may be detrimental, since it will alert a predator from the presence of a nest. Alarm calling, may also reveal the position of the signaller, increasing the risk of predation to adults (Klump et al. 1986, Wood et al. 2000). Wrens may be forced to assume greater risks when nestling are young due to their higher vulnerability to the lack of parental care but as offspring become older, the cost of resuming parental duties in the presence of a threat would be higher relative to the marginal benefit obtained. Hence, as nestlings develop, it may pay for parents to adopt a less risky form of parental care, such as alarm calling to distract/deter predators or to reduce nestling's activity to avoid being detected. Specific experiments to test the function and effectiveness of parent's alarm calling would be necessary to confirm this hypothesis.

CONCLUSION

Nest defence and parental risk-taking behaviours are usually seen as the result of a trade-off between current and residual reproductive value of broods. This trade-off involves factors such as annual fecundity, survival probability, offspring vulnerability, and re-mating and re-nesting potential of breeding individuals. However, the relationship among these vital parameters is far from simple. Dale et al. (1996) showed that these relationships vary with nesting stage and offspring condition, and therefore decision rules could change along the nesting cycle. In this study we found that breeding individuals took greater risks when raising a brood with young nestlings than when rearing old nestlings, but they increased alarm calling as nestling became older. The risk-taking behaviour House Wrens display agree with the expected under the "risk of harm-to offspring" hypothesis, but increased alarm calling appear to respond to an increase in the brood's reproductive value. As nestlings grow, their requirements change, and, consequently, it may cause a reduction of the benefits for the parents generated by assuming riskier behaviours such as entering the cavity to feed the young when there is a predator in the vicinity. We think that these results are, therefore, not contradictory, and that the parent decisions to assume a risk and/or to defend offspring could be still explained by the trade-off between the marginal value obtained from these behaviours and the associated costs in terms of the reduction in the residual reproductive success in accordance to the life history theory.

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STRESZCZENIE

[Podejmowanie ryzyka i obrona gniazda u strzyżyka śpiewnego]

U ptaków krótko żyjących podejmowanie podczas okresu opieki nad pisklętami działań obarczonych ryzykiem zranienia lub śmierci często jest rozpatrywane w odniesieniu do potencjału rozrodczego potomstwa (tzw. hipoteza „potencjału lęgu") oraz negatywnych skutków, jakie może powodować brak opieki rodzicielskiej (tzw. hipoteza „ryzyka zagrożenia dla potomstwa"). Hipoteza „potencjału lęgu" zakłada, że ryzyko podejmowane przez dorosłe ptaki oraz inwestycje w obronę gniazda powinny wzrastać wraz z wiekiem oraz liczbą piskląt w lęgu, natomiast hipoteza druga, że powinny być najwyższe, gdy pisklęta wymagają szczególnej opieki (m.in. ogrzewania, gdyż nie mają jeszcze zdolności termoregulacji), tzn. w początkowym okresie po wykluciu.

W pracy oceniano podejmowanie ryzyka i obronę gniazda przez samce i samice strzyżyka śpiewnego gniazdującego w skrzynkach lęgowych. Przy gniazdach umieszczano model puchacza wirginijskiego, który jest drapieżnikiem dorosłych strzyżyków, ale nie stanowi zagrożenia dla piskląt w gnieździe. Eksperymenty wykonano w dwóch okresach: gdy strzyżyki karmiły bardzo młode (3–4 dniowe, pozbawione zdolności termoregulacji) oraz starsze (10–12 dniowe) pisklęta. Przeanalizowano zachowanie ptaków dorosłych w ciągu 1 h przed umieszczeniem modelu puchacza, a następnie w ciągu 0,5 h po jego umieszczeniu. Jako reakcję ptaków określano czas, jaki upłynął od momentu wystawienia modelu do momentu wejścia do skrzynki/podjęcia karmienia przez ptaki, oraz czas, jaki ptaki spędzały na wydawaniu dwóch rodzajów głosów zaniepokojenia (Fig. 1), co zostało uznane za wskaźnik obrony gniazda.

W obecności modelu puchacza strzyżyki wracały do obowiązków rodzicielskich później niż przed jego umieszczeniem (Fig. 2A). Samice podejmowały obowiązki rodzicielskie częściej niż samce oraz czyniły to szybciej w przypadku małych piskląt (Fig. 2B), co potwierdza hipotezę „ryzyka zagrożenia dla potomstwa". Z drugiej strony czas spędzony na wydawaniu głosów zaniepokojenia wzrastał wraz z wiekiem piskląt (Fig. 3), co jest zgodne z hipotezą „potencjału lęgu" (Fig. 3). Tak więc gniazdujące strzyżyki reagują zarówno na potrzeby piskląt, jak i potencjał rozrodczy lęgu, gdyż podejmują większe ryzyko, kiedy pisklęta są małe oraz intensywniej bronią gniazda, gdy pisklęta są starsze.