

Injury feigning in the Savanna Nightjar: a test of the vulnerability and brood value hypotheses

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Received: 8 October 2015 / Revised: 5 August 2016 / Accepted: 12 September 2016 / Published online: 27 September 2016
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Abstract Nest predation is a major threat to the survival of young birds and is thus a crucial selective pressure influencing the evolution of life history traits. Injury feigning is a nest-defense mechanism in which the parents attract the attention of predators to secure their offspring. Because parents may incur a cost from injury feigning, they should adjust their injury-feigning behavior to different situations to maximize fitness. In this study, we used the Savanna Nightjar, *Caprimulgus affinis*, as a model organism to test the vulnerability and brood value hypotheses for predicting the occurrence of injury-feigning behavior. A field study was performed between 2006 and 2012, and observations were recorded from 123 nests. Both nestling movement and injury feigning increased after hatching, reached their peak at a nestling age of 8–10 days, and then declined afterward.

In addition, the frequency of injury feigning by the female differed between habitats, being higher in a low-plant-cover habitat than in a high-plant-cover habitat. Both findings are consistent with the vulnerability hypothesis. By contrast, the intensity of injury-feigning behavior did not linearly increase with nestling age and brood size; thus, the brood value hypothesis was not supported.

Keywords *Caprimulgus affinis* · Injury feigning · Brood value hypothesis · Vulnerability hypothesis

Zusammenfassung

Das Vortäuschen von Verletzungen bei der Savannen-Nachtschwalbe (*Caprimulgus affinis*): ein Test der “vulnerability hypothesis” und der “brood value hypothesis”

Communicated by O. Krüger.

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Electronic supplementary material The online version of this article (doi:10.1007/s10336-016-1400-0) contains supplementary material, which is available to authorized users.

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Nesträuber sind eine Hauptbedrohung für das Überleben von Jungvögeln und stellen somit einen sehr wichtigen Selektionsdruck für die Entwicklung von “life history traits” (Verhaltensmerkmale in der Lebensgeschichte) dar. Verletzungen vorzutäuschen ist dabei ein Verteidigungsmechanismus für das Nest, bei dem die Elterntiere die Aufmerksamkeit des Nesträubers auf sich ziehen und so ihre Jungen in Sicherheit bringen. Weil das Vortäuschen von Verletzungen den Elterntieren gewisse “Investitionskosten” verursacht, sollten sie die Ausprägung dieser Verhaltensweise an unterschiedliche Situationen anpassen können, um die “fitness”, das Kosten-Nutzen-Verhältnis, zu maximieren. In unserer Untersuchung benutzten wir die Savannen-Nachtschwalbe (*Caprimulgus affinis*) als Modell-Organismus, um zu testen, wie weit die “vulnerability hypothesis” und/oder

die “brood value hypothesis” geeignet sind, das Auftreten von Verletzungsvortäuschung vorherzusagen. Von 2006 bis 2012 wurden Freilandbeobachtungen an 123 Nestern aufgezeichnet. Sowohl das Bewegen der Nestlinge als auch das Vortäuschen von Verletzungen wuchs nach dem Schlüpfen an, erreichte den höchsten Wert, als die Nestlinge acht bis zehn Tage alt waren und ging dann wieder zurück. Außerdem hing beim Weibchen die Häufigkeit dieses Verhaltens vom umgebenden Habitat ab: in niedrigem Bewuchs trat es häufiger auf als in Habitaten mit hohem Bewuchs. Beide Ergebnisse unterstützen die “vulnerability hypothesis”. Die Intensität des Täuschungsverhaltens stieg dahingegen nicht linear mit dem Alter der Nestlinge oder der Gelegegröße an; somit wird die “brood value hypothesis” von unseren Ergebnissen nicht unterstützt.

Introduction

Nest predation is a major threat to nestling survival and therefore is a crucial selective pressure influencing the evolution of life history traits (Ricklefs 1969; Breitwisch 1988; Martin et al. 2000). Parental birds use various strategies to protect their nestlings in the presence of potential predators (Brunton 1986; Grubb 1998). Because nest defense may be risky (Montgomerie and Weatherhead 1988), parents often encounter a tradeoff between their current brood and their own survival, which is associated with future reproductive opportunities (Williams 1966; Ghalambor and Martin 2001; Fontaine and Martin 2006). Thus, parents should optimize their behavior when experiencing threats to ensure maximum fitness (Williams 1966; Charnov and Krebs 1974).

Distraction display is a common defense behavior exhibited by nesting birds to divert the attention of potential predators from the nestlings (Armstrong 1954). Injury feigning, where birds act crippled or injured, is one of the most common forms of distraction display, effectively leading predators away from the nestlings (Tomkins 1942; Bengtson 1970; Steyn 1971; Hobbs 1972; Brunton 1990; Byrkjedal 1991). Although injury-feigning behavior can increase the survival chances of offspring (Byrkjedal 1987), the parent bird may incur some costs, such as being killed by predators or energy expenditure (Brunton 1986, 1988, 1990). Thus, parent birds should adjust the frequency of injury-feigning behavior to attain a balance between the benefits and costs during the breeding season.

The frequency of injury feigning often changes during the breeding season (Andersson et al. 1980; Burger et al. 1989; Brunton 1990). The vulnerability and brood value

hypotheses have been proposed for explaining the temporal changes in the frequency of injury feigning, and these two hypotheses are not mutually exclusive. According to the vulnerability hypothesis, the intensity of nest defense correlates with the vulnerability of broods to predation (Burger et al. 1989; Redondo and Carranza 1989; Brunton 1990; Onnebrink and Curio 1991). For altricial birds, chick vulnerability tends to increase until fledging, and nest defense may increase with nestling age and peak immediately prior to fledging (Brunton 1990; Barash 1975). For precocial species, the mobility and survival potential of offspring increases rapidly within a few days after hatching (Barash 1975). Parental defense for precocial species should increase after hatching, and then gradually decrease until the hatchlings become fledglings and can protect themselves (Brunton 1990; Barash 1975). On the other hand, according to the brood value hypothesis, the parents take more risk in defending older or otherwise more valuable broods (Winkler 1987; Montgomerie and Weatherhead 1988; Jukkala and Piper 2015). The survival rate and probability of reaching reproductive age generally increase with brood age (Patterson et al. 1980). Although these two hypotheses were proposed more than two decades ago, only a few empirical studies, namely studies on Killdeer (*Charadrius vociferous*), Zenaida Doves (*Zenaida aurita*), and Red Grouse (*Lagopus lagopus scoticus*) (Burger et al. 1989; Brunton 1990; Hudson and Newborn 1990), have tested these hypotheses in the context of injury-feigning behavior. The results from these three studies were consistent with the vulnerability hypothesis, but did not support the brood value hypothesis.

In this study, we used the Savanna Nightjar, *Caprimulgus affinis*, a precocial bird species, as a model to test the vulnerability and brood value hypotheses. We performed a field test and recorded the movements of nestlings, age of female Nightjars and nestlings, brood size, and occurrence of injury-feigning behavior during the breeding season in low-plant-cover and high-plant-cover habitats. According to the vulnerability hypothesis, we predict that:

1. The frequency of injury feigning by female Nightjars is higher in low-plant-cover habitat than in high-plant-cover habitat.
2. The frequency of injury feigning by female Nightjars increases with an increase in the frequency of nestling movement.
According to the brood value hypothesis, we predict that:
3. The frequency of injury feigning by female Nightjars increases with the number of offspring.

Moreover, if brood value has a greater impact on injury-feigning behavior than brood vulnerability, then the

frequency of injury feigning should increase throughout the nesting cycle and peak immediately prior to fledging, with a linear nestling age-related trend. But if the vulnerability of nestlings is more influential, then injury feigning should peak around hatching and decrease before the fledging stage, with a quadratic nestling-age-related trend.

Materials and methods

Study areas

The experiment was conducted in two habitats, riverbanks (high plant cover) and urban rooftops (low plant cover) in Taichung, Taiwan, from 2006 to 2012. The riverbank habitat included the Wu River and its tributaries, the Dali and Caohu Rivers. Most of the Savanna Nightjar nests were located on riverbanks with 25–50 % plant cover (Fig. S1a). The urban rooftop habitat included rooftops of government agencies and schools with little human disturbance. The main building materials were cement and heat-resistant bricks (Fig. S1b, c).

Study species

The Savanna Nightjar (*Caprimulgus affinis* Horsfield 1821) is widely distributed in central and south China, Pakistan, India, Indonesia, and Taiwan (Hoyo and Bierregaard 1999; Brazil and Nurney 2010). In Taiwan, the breeding season of the Savanna Nightjar typically begins in late February to mid-March and ends in June (Lin and Wang 2009). The female parent incubates eggs and feeds the nestlings, and the male parent guards the nest (Lin and Wang 2009). Injury-feigning behavior has been observed only in females when they were approached by humans or predators (Lin and Wang 2009).

General field methods

Savannah Nightjar nests were monitored at night by using flashlights before initiating behavioral assays. Mist nets were used to capture females, and the captive birds were marked with uniquely numbered aluminum rings. The age of the mother was estimated according to banding records beginning from 2005 (acquired from the Taichung Wildlife Conservation Group, Taichung, Taiwan) or age-related wing morphology (Fig. S2 and Table S1; Gargallo 1994). Of the female parents used in the behavior assays, 14.6 % were banded when they were chicks; therefore, their ages were estimated using banding records. The ages of the remaining individuals were estimated on the basis of traits including the hue and amount of speckles on the head, coverts, and flight feathers (Fig. S2 and Table S1, Gargallo 1994). The female parents were divided into three age

classes: 1 year old (age class 1), 2 years old (age class 2), ≥ 3 years old (age class 3).

Behavioral assays were performed before the hatched nestlings became fledglings (approximate age 14 days). Injury-feigning behavior was evaluated by recording the reactions of the female parent to a human intruder. Every morning, the researchers approached the nests at a rate of 5 m/min until the female parent flew away. We tested each of the 123 nesting females 14 times (i.e., from the first day after hatching until the chicks were 14 days of age). The individual females were not tested repeatedly among study years. The presence or absence of injury-feigning behavior, and the reaction distance at which the bird performed injury-feigning behavior in response to the intruder, were recorded. After the female parent flew away, the researchers stood 3 m from the nest and observed whether the nestlings exhibited any spontaneous movements (horizontal movement over one nestling body length) within 5 min. The behavior data obtained in this study have been deposited in Zendo (doi:10.5281/zenodo.51070).

Statistical analysis

Generalized linear mixed models (GLMMs) were fitted using binomial outcomes of occurrence of injury-feigning behavior with a logit link function for evaluating factors potentially affecting the injury-feigning behavior. Fixed effects were the age of the female parent (age class 1, 2 or 3; numerical or categorical variable; see model details in Table S2), nestling age (1–14 days old; numerical variable) and its quadratic term (age^2), habitats type (riverbanks or urban rooftops; categorical variable), nestling movements (absence or presence; categorical variable), brood size (one or two nestlings; categorical variable), study year (2006–2012; categorical variable), interactions between habitat type and nestling age, between habitat type and quadratic nestling age, and between habitat type and maternal age. The individual identity of the female parent was included as a random effect to account for variation in individuals' intrinsic frequency of injury feigning (random intercepts) and different rates of change according to each nestling age or quadratic nestling age (random slopes). The factors potentially associated with the reaction distance of injury-feigning behavior were evaluated using linear mixed-effects models. The fixed effects in the model were the age of the female parent, age of the nestling, habitat type, nestling movements, brood size and year; the random effects were the random intercepts and slopes among individual females according to nestling age. In both analyses, we initially included all independent variables (full model) and removed independent variables sequentially according to Akaike's information criterion (AIC) (Akaike 1974; Dobson 2002). The model with the lowest AIC value was considered the optimum approximating model (final model) given the data,

and models with an AIC difference <2 were considered as competitive (Burnham and Anderson 2002). Likelihood ratio tests were used to evaluate model parsimony. Marginal and conditional coefficients of determination (R^2) of the final model were calculated by using the R^2 GLMM function of the MuMIn library (Bartoń 2014). A marginal R^2 represents the proportion of variance explained by the fixed effects alone, whereas a conditional R^2 represents the proportion of variance explained by both the fixed and random effects. All statistical analyses were conducted using R version 3.1.2 (R Core Team 2014), and the glmer and lme functions of the lme4 and nlme libraries, respectively, were used (Pinheiro et al. 2007; Bates et al. 2014). The average marginal predicted probabilities of occurrence of injury-feigning behavior from the most parsimonious model were calculated by using predict function in lme4.

Results

General description

We recorded observations from 123 nests, of which 69 were on riverbanks and 54 were on urban rooftops. Of the 123 nests, 32 nesting females belonged to age class one, 42 females belonged to age class 2, and 49 females belonged to age class 3. Most nests contained two nestlings; 104 nests contained two nestlings, and 19 nests contained one nestling. Of the 1722 observations, injury-feigning behavior was recorded 308 times (17.9 %; Table 1). Most female Nightjars (116 of 123, 94.3 %) displayed injury-feigning behavior at least once during the experimental period. We never observed any injury-feigning behavior during occasional nest visits before hatching or after fledging.

Injury-feigning behavior on urban rooftops was first recorded when the nestlings were aged 4 days and reached minimal levels at 13 days (only one of 54 individuals still exhibited injury-feigning behavior on days 13 and 14), whereas on riverbanks, the behavior was first recorded when the nestlings were aged 5 days and ceased at 13 days of age (Fig. 1). The proportions of the presence of injury-feigning behavior was higher on urban rooftops than on riverbanks during the experimental period, being 21.4 and 15.1 % for urban rooftops and riverbanks, respectively (Table 1). The

presence of injury-feigning behavior at each nestling age ranged from 0 to 61.1 %, with an average of 18.3 % (Fig. 1a). Nestling movements were recorded at the nestling age of 4–11 days for rooftop-habitat nestlings and 2–14 days for riverbank nestlings (Fig. 1b). The presence of nestling movements at each nestling age ranged from 0 to 33.3 %, with an average of 10.9 %.

Occurrence of injury-feigning behavior

The model with the fixed effects of the linear and quadratic effect of nestling age, the numerical age of the female parent, habitat type, and the interaction between habitat type and linear nestling age was the most parsimonious (AIC weight 0.469; Table 2). According to the strength of evidence provided by the Δ AIC and the relative likelihoods (Table 2), the models including the interaction between habitat type and quadratic nestling age, and between habitat type and maternal age, are also highly qualified to explain the data. The results of these two alternative models and the full model are listed in the Supplementary Material, Tables S3 and S4. Among the four fixed effects in the final model, nestling age had the strongest influence on the occurrence of injury feigning (Fig. 2). Nestling age had a significant quadratic effect on injury-feigning behavior ($P < 0.0001$; Table 3; Fig. 2a). The predicted probability of the presence of injury feigning at each nestling age ranged from 2.76×10^{-5} to 0.49. The predicted probability increased with maternal age, and the probability for maternal age class 3 was 0.21, which was 0.7 times greater than that for maternal age class 1 ($P < 0.0001$; Tables 2, 3; Fig. 2b). Overall, the observed proportion of older females exhibiting injury feigning was higher than that of younger females at each nestling age (Fig. 1c). The predicted probability of the presence of injury-feigning behavior was different between habitats, being more frequent on rooftops (0.21) than on riverbanks (0.15) ($P < 0.0001$ Tables 3; Fig. 2c). There was a significant two-way interaction between habitat type and nestling age for the occurrence of injury feigning (Table 3). Although the temporal change in the frequency of injury feigning synchronized with the change in the frequency of nestling movement (Fig. 1a, b), nestling movement was excluded from the final model. This may be attributed to the collinearity between nestling

Table 1 Number of injury-feigning-behavior (IFB) observations in two habitats among maternal age classes

| Maternal age classes (years) | Rooftop | | Riverbank | |
|------------------------------|--------------|-------------|--------------|-------------|
| | IFB presence | IFB absence | IFB presence | IFB absence |
| 1 | 31 | 179 | 29 | 209 |
| 2 | 55 | 211 | 46 | 276 |
| 3 | 76 | 204 | 71 | 335 |
| Total counts | 162 | 594 | 146 | 820 |

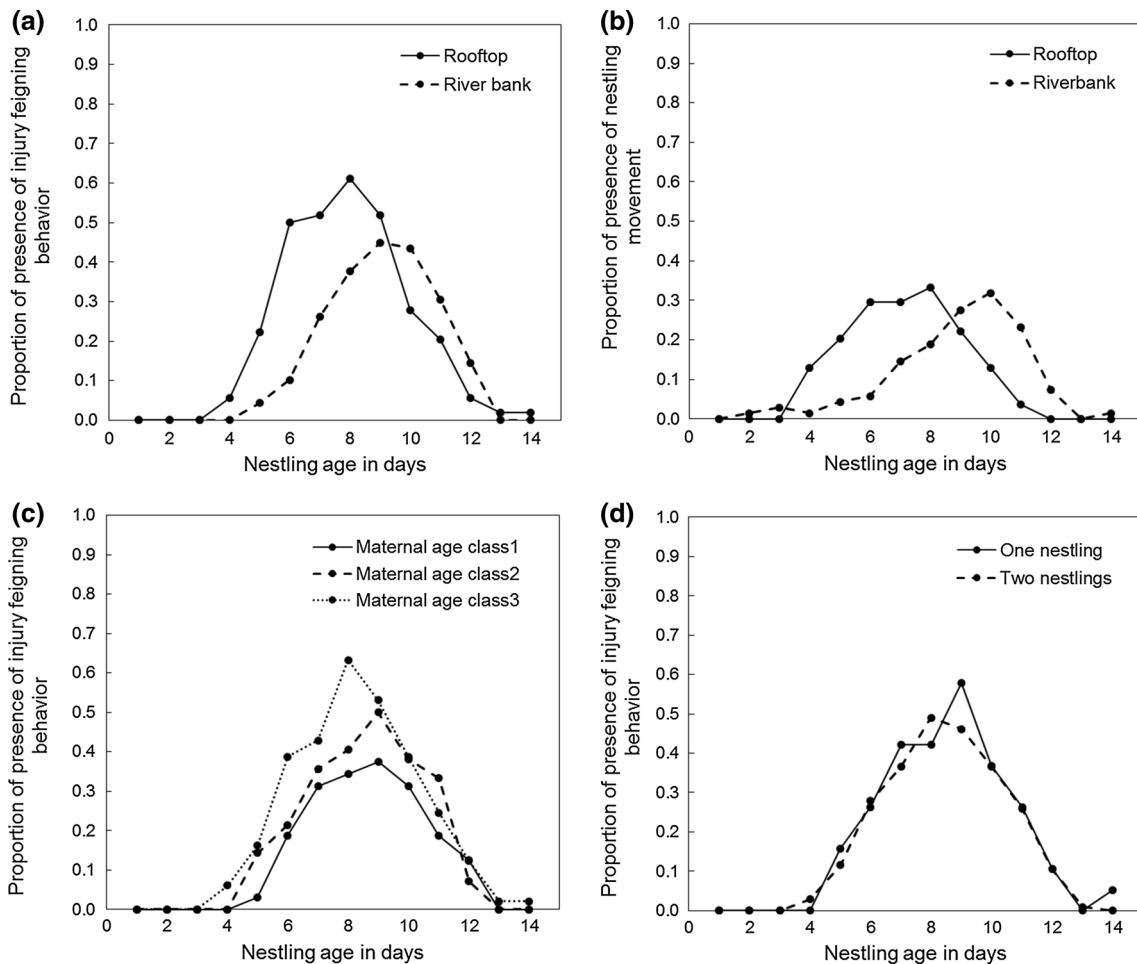


Fig. 1 **a** Proportion of female Nightjars exhibiting injury-feigning behavior relative to nestling age in rooftop and riverbank habitats; **b** proportion of nests exhibiting nestling movement relative to nestling age in rooftop and riverbank habitats; **c** proportion of female

Nightjars of three different age classes exhibiting injury-feigning behavior relative to nestling age; **d** proportion of female Nightjars with one nestling and two nestlings exhibiting injury-feigning behavior relative to nestling age

movement and quadratic nestling age (Table S6). Brood size was also excluded from the final model (Table 1). The observed proportion of female parents with one nestling exhibiting injury feigning was similar to that of female parents with two nestlings (Fig. 1d). The marginal and conditional R^2 -values of the final model were 77.9 and 80.9 %, respectively, indicating that the random effects add very little to the overall explained deviance in this analysis. The variation in injury-feigning behavior among individual female Nightjars was not high.

Reaction distance of injury-feigning behavior

The reaction distance of injury-feigning behavior ranged from 3 to 12 m, with a mean distance of 6.5 m. Although the model including maternal age classes had the lowest AIC value which suggests this model was more parsimonious than the others (Table 4), the likelihood ratio test revealed that the model including the random effects and maternal age

was not significantly from the null model including only the random effects and intercept in explaining variation in reaction distance ($\chi^2 = 2.0928, P = 0.148$). The results of the full model are listed in the Supplementary Material, Tables S5. None of the factors in our model, the nestling and maternal ages, nestling movement, habitat type, brood size, and year, exerted significant effects on the reaction distance of injury-feigning behavior (Table 4). The average reaction distance in the two habitats was equal (6.5 m). The reaction distance slightly decreased with maternal age, with the averages being 6.9, 6.5, and 6.4 m; however, the differences were not statistically significant.

Discussion

The vulnerability hypothesis proposes that parents exhibit intense nest-defense behavior when their broods are at a vulnerable stage (Burger et al. 1989; Redondo and

Table 2 Generalized linear mixed-model-fitting results for the occurrence of injury-feigning behavior

| Response variable | Random effects | Fixed effects | AIC | Δ AIC | Relative likelihood | Akaike weight |
|---|--|---|--------|--------------|---------------------|---------------|
| Injury-feigning behavior (presence/absence) | (Nestling age femaleID) + (nestling age ² femaleID) ^a | Nestling age ² + nestling age + maternal age (C) ^b + nestling movement + habitat + Year + Brood size + habitat × nestling age + habitat × nestling age ² + habitat × maternal age (C) (full model) | 1148.4 | 22.2 | <0.001 | <0.001 |
| | (Nestling age femaleID) | Nestling age ² + nestling age + maternal age (N) ^c + habitat + habitat × nestling age (final model) | 1126.2 | 0.0 | 1.000 | 0.469 |
| | (Nestling age femaleID) | Nestling age ² + nestling age + maternal age (N) + habitat + habitat × Nestling age + habitat × nestling age ² | 1126.9 | 0.7 | 0.705 | 0.330 |
| | (Nestling age femaleID) | Nestling age ² + nestling age + maternal age (N) + habitat + habitat × Nestling age + habitat × nestling age ² + habitat × maternal age (N) | 1127.9 | 1.7 | 0.427 | 0.200 |

Only the full model and models with Δ Akaike's information criterion (AIC) <2 are presented. More complete results for each analysis are shown in Supplementary material, Table S2

ID Identity

^a (Nestling age|FemaleID) represents the random effects for the intercepts and slopes among individuals according to linear nestling age, and (Nestling age²|FemaleID) represents the random effects for the intercepts and slopes among individuals according to quadratic nestling age

^b Maternal age was treated as a categorical variable

^c Maternal age was treated as a numerical variable

Carranza 1989; Brunton 1990; Onnebrink and Curio 1991). Our results indicate that nestling age had the strongest influence on the occurrence of injury feigning, with a quadratic nestling age-related trend. In our field experiment, the nestlings rarely moved before the age of 4 days, and the nestlings' brown, bark-like plumage enabled them to blend in with the surroundings. Hence, when human intruders disturbed the nests at this stage, the female parent directly flew away without displaying injury feigning. Being precocial, Savanna Nightjar chicks are mobile only a few days after hatching. The nestlings became active after the age of 4 days. The female parent displayed injury feigning more often at this stage, and the broods were now more conspicuous to the predators. As soon as the Savanna Nightjar nestlings became fledglings, the injury-feigning behavior of the female parent was no longer needed because the fledglings were able to fly and protect themselves. In addition, the female parent displayed injury feigning more frequently in the low-plant-cover habitat, where predators might have detected the brood more easily. Studies on the Red Grouse, *L. lagopus scoticus* and American Robin, *T. migratorius*, have reported similar relationships between the degrees of nesting cover and nest-defense intensity (McLean et al. 1986; Hudson and Newborn 1990). The intensity of distraction displays of the male Red Grouse was negatively correlated with vegetation height (Hudson and Newborn 1990), whereas extreme

distraction displays were more frequent in American Robins with poorly concealed nests than in those with well-concealed nests (McLean et al. 1986).

Our results do not support the brood value hypothesis. The occurrence of injury feigning by the female Nightjar showed a significant quadratic relationship rather than a linear relationship with nestling age. Female Nightjars with two nestlings did not perform injury feigning more frequently than female Nightjars with one nestling. An association between the intensity of brood defense and the number of offspring has been demonstrated in many avian species (Thornhill 1989; Wiklund 1990; Jukkala and Piper 2015). However, some findings did not support the brood value hypothesis (Tryjanowski and Goławski 2004). In a study on Eurasian Kestrels (*Falco tinnunculus*), the nest-defense intensity of females increased with offspring number at the incubation stage but not at the nestling stage (Tolonen and Korpimäki 1995). In a study on the Red-backed Shrike (*Lanius collurio*), the intensity of nest defense increased with the brood age, but not with the number of offspring (Tryjanowski and Goławski 2004). The frequency of injury feigning by the Savanna Nightjar increased neither linearly with nestling age nor with the number of nestlings; therefore, the vulnerability hypothesis provides a more likely explanation for the variation in injury feigning of the Savanna Nightjar than the brood value hypothesis.

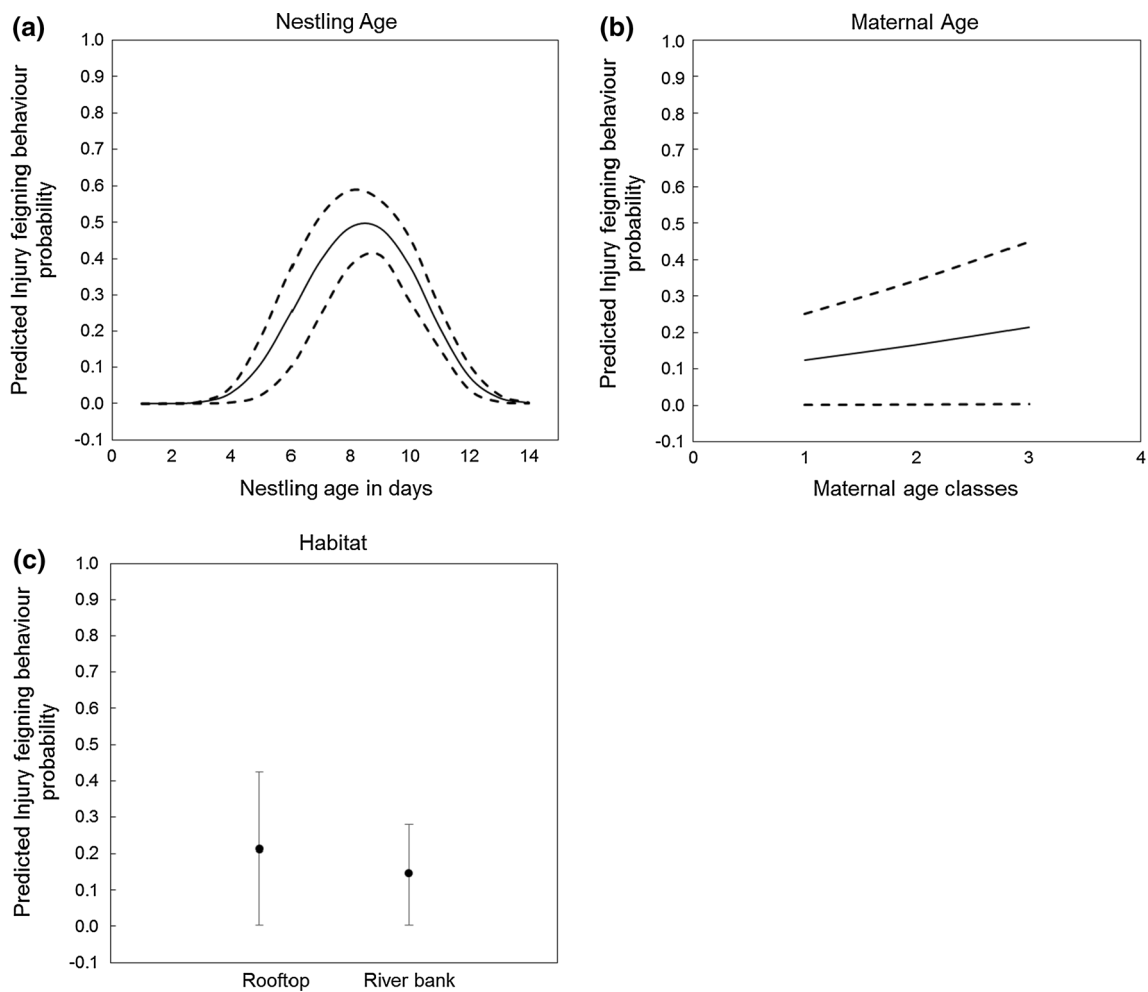


Fig. 2 Predicted probability of the presence of injury-feigning behavior in Savanna Nightjars as a function of **a** nestling age, **b** maternal age, and **c** habitat type. *Solid lines and points* represent the

average marginal predicted probabilities from the most parsimonious model. *Dashed lines and error bars* represent upper and lower quartiles of the predicted values

Table 3 Parameter estimates for the most parsimonious model of the occurrence of injury-feigning behavior

| Response variable | Independent variables | | | | |
|---|----------------------------------|-------------------|------|----------|---------|
| | Fixed effects | Estimate | SE | Z-value | p-value |
| Injury-feigning behavior (presence/absence) | Intercept | -13.65 | 1.21 | -11.29 | <0.0001 |
| | Nestling age (days) | 3.33 | 0.29 | 11.37 | <0.0001 |
| | Nestling age ² (days) | -0.21 | 0.02 | -11.57 | <0.0001 |
| | Maternal age ^a | 0.44 | 0.10 | 4.31 | <0.0001 |
| | Habitat(riverbank) | -4.55 | 0.75 | -6.05 | <0.0001 |
| | Habitat × nestling age | 0.46 | 0.09 | 5.28 | <0.0001 |
| | Random effects | | | Variance | SD |
| Injury-feigning behavior (presence/absence) | Random intercepts | Individual female | | 1.68 | 1.30 |
| | Random slopes | Nestling age | | 0.03 | 0.18 |

^a Maternal age was treated as a numerical variable

Table 4 Linear mixed-effects-model-fitting results for reaction distance

| Response variable | Random effect | Fixed effects | AIC | Δ AIC | Relative likelihood | Akaike weight |
|-------------------|--------------------------------------|---|--------|--------------|---------------------|---------------|
| Reaction distance | (Nestling agelfemaleID) ^a | Nestling age + maternal age (C) ^b + nestling movement + habitat + year + brood size (full model) | 1308.5 | 17.9 | <0.001 | <0.001 |
| | (Nestling agelfemaleID) | None (final model) | 1290.7 | 0.1 | 0.951 | 0.224 |
| | (Nestling agelfemaleID) | Maternal age (N) ^c | 1290.6 | 0.0 | 1.000 | 0.236 |
| | (Nestling agelfemaleID) | Brood size | 1291.7 | 1.1 | 0.577 | 0.136 |
| | (Nestling agelfemaleID) | Maternal age (C) | 1292.1 | 1.5 | 0.472 | 0.111 |
| | (Nestling agelfemaleID) | Nestling age | 1292.2 | 1.6 | 0.449 | 0.106 |
| | (Nestling agelfemaleID) | Nestling movement | 1292.3 | 1.7 | 0.427 | 0.101 |
| | (Nestling agelfemaleID) | Habitat | 1292.7 | 2.1 | 0.350 | 0.083 |
| | (Nestling agelfemaleID) | Year | 1300.3 | 9.7 | 0.008 | 0.002 |
| | (Nestling agelfemaleID) | Nestling movement + year | 1302 | 11.4 | 0.003 | 0.001 |
| | (Nestling agelfemaleID) | Nestling age + nestling movement + year | 1303.5 | 12.9 | 0.002 | <0.001 |
| | (Nestling agelfemaleID) | Nestling age + maternal age (N) + nestling movement + habitat + year | 1305.1 | 14.5 | 0.001 | <0.001 |
| | (Nestling agelfemaleID) | Nestling age + nestling movement + habitat + year | 1305.3 | 14.7 | 0.001 | <0.001 |
| | (Nestling agelfemaleID) | Nestling age + maternal age (N) + nestling movement + habitat + year + brood size | 1306.6 | 16.0 | <0.001 | <0.001 |

^a The individual identity of the female parent was used as a random effect (random intercepts and slopes among individuals according to nestling age)

^b Maternal age was treated as a categorical variable

^c Maternal age was treated as a numerical variable

Our results indicate that older female Nightjars displayed injury feigning more often than younger conspecifics (Tables 2, 3; Figs. 1c, 2b). The age effect on injury feigning may be interpreted from two perspectives. Maternal experience in breeding and brood defense increased with age, whereas their residual reproductive value declined with age (Nur 1984; Montgomerie and Weatherhead 1988; Thornhill 1989). Parental experience may improve brood survival; thus, broods are more valuable for experienced parents. In addition, the cost of defense may decrease because of increased experience acquired from previous challenges. Thus, age-related injury feigning may be attributed to differences in the parental experience of female Nightjars (Nur 1984; Montgomerie and Weatherhead 1988; Thornhill 1989). When female survival ability and fecundity decrease with age, increased parental care (e.g., injury feigning) is expected because residual reproductive value declines (Williams 1966; Montgomerie and Weatherhead 1988).

This study provides evidence to support the vulnerability hypothesis regarding the occurrence of injury feigning in the Savanna Nightjar. Injury feigning may have a selective advantage in birds nesting in open and exposed places (Armstrong 1954). Caprimulgids usually lay their eggs on the ground in an open environment without constructing nests (Colebrook-Robjent 1984; Ingels et al.

1984; Tiwari and Dadu 2010; Solano-Ugalde et al. 2012). However, the timing of injury feigning varies among species of the Caprimulgidae family. For example, the male Swamp Nightjar (*Caprimulgus natalensis*) and Blackish Nightjar (*Caprimulgus nigrescens*) display injury-feigning behavior during the incubation period (Ingels et al. 1984; Hustler and Mitchell 1997), whereas the Savanna Nightjar and Freckled Nightjar (*Caprimulgus tristigma*) display this behavior only during the nestling period (Steyn 1971). Injury feigning was observed in both male and female Silky-tailed Nightjar individuals (*Caprimulgus sericocaudatus mengeli*) (Wilkinson 2009), whereas it was observed only in the female Savanna Nightjar. These behavioral differences may be attributed to differences in the predation risk during each stage of the nesting period and parental role division between the sexes in each species. For example, injury feigning in the Blackish Nightjar during the incubation period may reflect the fact that eggs are the most vulnerable stage in this species' development (Skutch 1972; Ingels et al. 1984). Additional comparative studies are required and may provide valuable insights into the evolution of the distraction behavior of avian species.

Acknowledgments We are grateful to Shue-Ru Wu and Tzu-Yang Lin for helping with the fieldwork. We would like to thank Pei-Jen Lee Shaner for valuable comments on the statistical analysis. This research was funded by the Taiwanese Forestry Bureau (97-18) and

Taichung City Government. None of the funders had any influence on the content of the submitted or published manuscript. None of the funders required approval of the final manuscript for it to be published.

Compliance with ethical standards

All applicable international, national, and institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest.

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