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Snake slough in birds' nests acts as a nest predator deterrent

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The use of snake slough as nest material by birds is considered an adaptive behavior to avoid nest predation. Here, we conducted predation experiments to test the hypothesis that the snake slough in nests of crested mynas (*Acridotheres cristatellus*) had anti-predatory effects. We put snake slough and white-rumped munia (*Lonchura striata*) eggs in the nest boxes to compare egg predation by Swinhoe's striped squirrels (*Tamiops swinhoei*), one of the main predators of cavity-nesting birds. In addition, we conducted experiments to examine if Swinhoe's striped squirrels identified the snake sloughs in the nest by vision or olfaction, and if the length of snake sloughs has effect on the predation rate. Our results showed that in the anti-predatory experiment, the egg predation rate (on days 3, 6) and the predation rate at which the squirrels first arrived the nest box were significantly lower in the experimental group than in the control group. In the olfaction experiment, there was no significant difference in both the predation rate (on days 1, 3, 6) and the predation rate at which the squirrels first arrived the nest box between the two groups. In the vision experiment, the predation rate at which the squirrels first arrived the nest box was significantly lower in the experimental group (hung snake slough) than in the control group (hung cotton strip). In the slough length experiment, the length of snake slough did not have a significant effect on the predation rate. These results suggest that the snake sloughs in bird nests can effectively deter nest predators, mainly via visual effect. Our study provided strong experimental evidence for the hypothesis that snake slough in birds' nests acts as a nest predator deterrent.

KEY WORDS: anti-predatory effect, crested myna, nest predation, snake slough, Swinhoe's striped squirrel.

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INTRODUCTION

Nest predation is one of the main causes of breeding failure in the majority of bird species (Ricklefs 1969; Skutch 1985; Martin 1993, 1995; Newton 1998; Lima 2009; Ibáñez-Álamo et al. 2015; DeGregorio et al. 2016; Fu et al. 2016). It is also an important selection pressure that affects the evolution of birds' life history characteristics (Martin 1988, 1995; Chase et al. 2002; Marini 2011). To avoid nest predation and improve their fitness, birds have evolved a series of anti-predatory strategies to reduce predation (Caro 2005), such as avoiding high-risk breeding habitats (Hua et al. 2013), reducing the number of offspring (Zanette et al. 2011), and minimizing movements in areas of high predation risks (Schneider & Griesser 2015). In addition, research in the field showed that some birds add non-structural materials to their nests to reduce the risk of nest predation. For example, birds add lichens, moss, and silk to strengthen or camouflage their nests and confuse the predators' visual perception, thereby reducing the chance of their eggs or chicks being spotted (Collias & Collias 1984). In addition, Schuetz (2004) found that common waxbills (*Estrilda astrild*) deter nest predators by the smell of carnivore manure that they add to their nests, thereby reducing nest predation. Moreover, Medlin and Risch's (2006) experiment verified that the snake slough in the nests of great crested flycatchers (*Myiarchus crinitus*) can deter predators, especially the Southern flying squirrels (*Glaucomys volans*).

Birds avoid predator traces. For example, the great tit (*Parus major*) avoids inhabiting nest boxes that contain predators' hair (Ekner & Tryjanowski 2008) and odors (Amo et al. 2011). During the breeding season, birds avoid predators' dens or nests, such as those of the red fox (*Vulpes vulpes*) (Tryjanowski et al. 2002) and the common kestrel (*Falco tinnunculus*) (Norrdahl & Korpimäki 1998; but see Norrdahl et al. 1995; Larsen & Grundetjern 1997). Snakes are common predators of birds' nests (Weatherhead & Blouin-Demers 2004; DeGregorio et al. 2014; Menezes & Marini 2017; Fulton 2018; Hendricks 2019; Savarino-Drago & Ruvalcaba-Ortega 2019). However, some avian species use snake slough as nest materials (Bolles 1890; Strecker 1926, 1927; Suthard 1927; Medlin & Risch 2006; Coppedge 2009; Alfréd & Prokop 2011; Dhandhukia & Patel 2012; Almeida et al. 2014). There have been records of birds using snake slough as nest material as early as the late 19th century (Bolles 1890), but to date, only two studies have explored the mechanism underlying the practice of birds using snake slough (Medlin & Risch 2006; Alfréd & Prokop 2011). Early scientists hypothesized that birds added snake slough to their nests (1) to provide a soft nesting material and (2) to deter predators (Bolles 1890; Strecker 1926). So far, only Medlin and Risch (2006) have confirmed with experiments that snake slough in bird nests reduces the possibility of nest predation. However, some questions remain unanswered regarding how predators detect snake slough and how much is needed to be effective.

Crested mynas (*Acridotheres cristatellus*) belong to the Passeriformes order and the Sturnidae family. They are common resident birds in southern China (Zheng 2017). Crested mynas are cavity-nesting birds, nests are mainly composed of hay, feathers, plastic paper, pine needles; some nests also contain snake slough (Feare & Craig 1998). During the breeding season from April to August 2018 and 2019, we observed crested mynas in Ding'an, tropical Hainan and found that they constantly added sloughs (not the entire slough, 2.0–18.3 cm) to their nest boxes throughout the breeding period (Fig. 1), a few of snake sloughs were hung on the branches near the nest entrance, and the average length of snake slough added to the nest were 4.11 ± 1.25 cm ($n = 12$) and 8.35 ± 6.04 cm ($n = 13$) in 2018 and 2019, respectively

Fig. 1. — Snake sloughs in nests of crested mynas during the breeding season [(a) refers to the egg-laying stage, (b) refers to the incubation stage and (c) refers to the nestling stage].

(J. Liu & W. Liang unpublished data). We hypothesized that the snake slough in mynas' nests could deter the nest predators in the same region (anti-predatory effect). To test this hypothesis, we examined the following aspects: (1) if snake slough has an anti-predatory effect; (2) the mechanism of the anti-predatory effect of the slough at the visual and olfactory levels; (3) the effect of the slough's length on the egg predation rate of the nest.

MATERIALS AND METHODS

Study area

This study was conducted in the south Longkun campus (19°59′N, 110°20′E) of Hainan Normal University in Haikou city, tropical Hainan island, China, from 2018 to 2019. The campus covers an area of about 26 ha, with main tree species on the campus including coconuts (*Cocos nucifera*), royal palms (*Roystonea regia*), orchid trees (*Bauhinia blakeana*), and Banyan figs (*Ficus microcarpa*) (Yang et al. 2009).

Nest box suspension and monitoring

Tit-type nest boxes were hung from the campus' trees. The dimensions of the nest boxes were according to the specifications proposed by Zhang et al. (2019). We investigated the density of squirrels before the experiment began. Based on our survey, the density of squirrels is quite high (2.6 individuals per ha; about 68 squirrels in the 26 ha of the campus) (J. Liu & W. Liang unpublished data). The nest boxes were suspended on tree trunks about 3 m from the ground in groups of two. The intra-group distance between the nest boxes was 15–25 m. The inter-group distance was greater than 60 m. To attract Swinhoe's striped squirrels (*Tamiops swinhoei*) to explore the nest boxes, we put 10 peanuts in each nest box 1 month before the experiment. The white-rumped munia eggs (1.01 ± 0.11 g in egg mass, 15.07 ± 0.80 mm in egg length, 11.29 ± 0.56 mm in egg width, n = 121) used in the experiment were all unfertilized eggs and were purchased online (Taobao Inc., Hangzhou, China). The snake sloughs used in the experiment (Chinese cobra, *Naja atra*) were obtained from a local farm. A WIFI/P2P miniature network camera (HD99S-32G, Shenzhen Skywork Digital Co.

Ltd, Shenzhen, China) with a portable battery (ROMOSS, Shenzhen Romoss Technology Co. Ltd, Shenzhen, China) as a continuous power supply was used inside of boxes for video recording to monitor the predators. In addition, the nests were monitored manually every afternoon. If the white-rumped munia eggs had bite marks or were missing during the experiment, they were considered to have been preyed upon. If at least one egg was preyed upon, the experiment was considered to be over and the nest box was removed immediately.

Anti-predatory experiment

A predator experiment (in area of high density of squirrels) was carried out before the anti-predatory experiment started. Only two white-rumped munia eggs were placed at the bottom of each nest box (n = 40). According to the results of the predator experiment, we found that the predators on the campus were all Swinhoe's striped squirrels by videos (ESM Video S1-S2), and the predation rate of the white-rumped munia eggs on day 6 was 97.5% (J. Liu & W. Liang unpublished data). Thus, the anti-predatory experiment period was set to 6 days.

Then, we investigated whether the snake slough in the nest boxes could deter the squirrels in November 2018. In the experiment (in area of high density of squirrels), nest boxes were grouped in two. In the experimental group (n = 12), snake slough (5–10 cm) and two white-rumped munia eggs were placed at the bottom of each nest box. In the control group (n = 12), gray cotton cloth strip of the same length as the snake sloughs and two white-rumped munia eggs were placed at the bottom of each nest box. After the experiment ended, we examined the videos and compared the squirrels' exploratory behavior of the nest boxes and the predation rate at which the squirrels first arrived the nest box between the two groups. We also examined the differences in the predation rates between the two groups on days 1, 3, and 6.

Olfaction and vision experiments

To explore the way in which Swinhoe's striped squirrels identified snake sloughs, we performed olfaction and vision experiments (in area of high density of squirrels) in December 2018 and January 2019; each experiment lasted 6 days. For the olfaction experiment, nest boxes were grouped in twos white-rumped munia eggs were placed in each nest box. In the experimental group (n = 12), a 10 cm slough was placed on the inner edge of the lid of the nest box so that it would not be visible to the squirrels. In the control group (n = 12), a 10 cm gray cotton strip was placed in the nest boxes. Similarly, in the vision experiment, nest boxes were grouped in twos white-rumped munia eggs were placed in each nest box. In the experimental group (n = 12), a 10 cm snake slough was hung at the opening of the nest box so that it covered 1/2 of the opening. In the control group (n = 12), a 10 cm gray cotton strip was hung at the same position as the snake slough on the nest box. After the experiment ended, we watched the videos and examined the differences in the predation rate at which the squirrels first arrived the nest box between the two groups. Additionally, we examined the differences in the predation rates by squirrels between the two groups on days 1, 3, and 6.

Slough length experiment

We observed that crested mynas added snake sloughs of different lengths to their nest boxes, the snake slough of 2019 was significantly longer than that of 2018. Thus, we suspect a potential effect of the snake slough length. To investigate the effect of slough length on Swinhoe's striped squirrels' egg detection and predation rates, we conducted a slough length experiment in October 2019. The experimental period was 12 days. The width of the sloughs was 2.5–4 cm. A total of 60 nest boxes, grouped in threes, were used in the experiment. At the bottom of each nest box, we placed either a 5 cm snake slough and two white-rumped munia eggs, a 10 cm snake slough and two white-rumped munia eggs, or a 20 cm snake slough and two white-rumped munia eggs. The differences in egg predation rates between the three groups on days 1, 3, 6, 9, and 12 were compared.

Data analysis

The differences among the egg predation rates and the latency by squirrels were analyzed using Fisher's exact test or Chi-square test. All tests were two-tailed, and the significance level was $P < 0.05$. The data are presented in the form of mean ± standard deviation (Mean ± SD). Data analysis was performed with the IBM SPSS 22.0 software (IBM Corp., Armonk, NY, USA).

RESULTS

Video processing and predator experiment

The recorded videos revealed that all the predators of the eggs in the nest boxes on campus were Swinhoe's striped squirrels. The squirrels exhibited different exploratory behaviors depending on whether the nest boxes contained snake sloughs or cotton strips. Nest boxes with snake sloughs were explored more times (ESM Video S1) than those with cotton strips (ESM Video S2), suggesting squirrels showed a tendency of fear towards nest boxes with snake sloughs.

Anti-predatory experiment

There was a significant difference in the nest predation rate between the experimental group and the control group and this increased with time (Fig. 2). The experimental group had no predation, but the predation rate of the control group was 25% on day 1. The predation rates of the experimental group were significantly lower than those of the control group on day 3 (Fisher's exact test, $\chi^2 = 8.711$, df = 1, $P = 0.009$, n = 24) and day 6 (Fisher's exact test, $\chi^2 = 9.882$, df = 1, $P = 0.005$, n = 24). In addition, the predation rate at which the squirrels first arrived the nest box was significantly lower in the experimental group than in the control group (Fisher's exact test, $\chi^2 = 13.594$, df = 1, $P = 0.001$, n = 24).

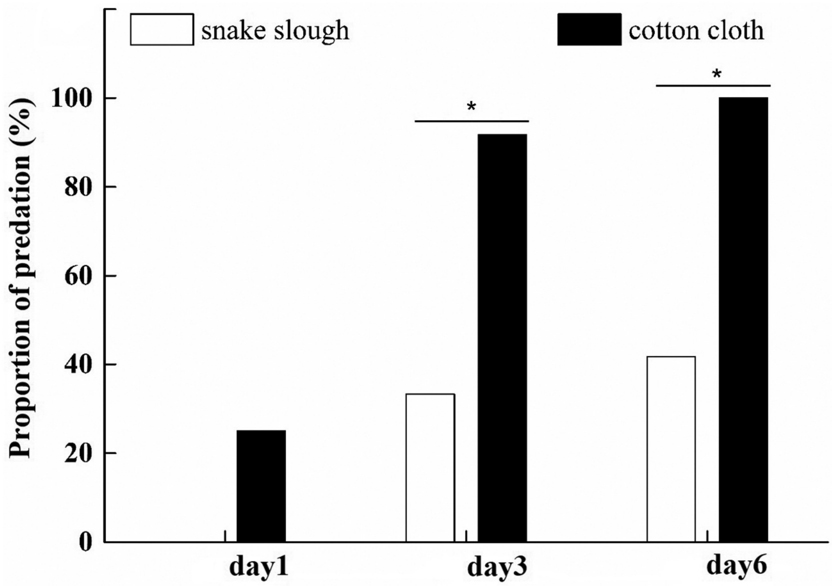

Fig. 2. — Changes in the predation rates of the snake slough group and the cloth strip group under different exposure times (* refers to statistical significance between the two groups).

Olfaction and vision experiments

The snake sloughs in the nests deterred Swinhoe's striped squirrels mainly through visual effects. In the olfaction experiment, there was no significant difference in the predation rate between the two groups (Fig. 3). Additionally, there was no significant difference in the predation rate at which the squirrels first arrived the nest box between the two groups (Fisher's exact test, χ^2 = 0.253, df = 1, P = 1, n = 24).

In the vision experiment, the predation rate of the experimental group was significantly lower than that of the control group on day 3 (Fisher's exact test, χ^2 = 6.750, df = 1, P = 0.027, n = 24) and there was no significant difference in the predation rate between the two groups on days 1 and 6 (Fisher's exact test, all P = 1, n = 24). However, the predation rate at which the squirrels first arrived the nest box was significantly lower in the experimental group than in the control group (Fisher's exact test, χ^2 = 8.711, df = 1, P = 0.009, n = 24).

Slough length experiment

Our results showed that the predation rate of the nests with different slough lengths increased with the time of exposure (Fig. 4). However, there were no significant differences in the nest predation rates on days 1, 3, 6, 9, and 12 (Chi-Square test, χ^2 = 2.105, df = 2, P = 0.349; χ^2 = 2.894, df = 2, P = 0.235; χ^2 = 0.15, df = 2, P = 0.928; χ^2 = 0.417, df = 2, P = 0.812; χ^2 = 0.404, df = 2, P = 0.817; n = 60).

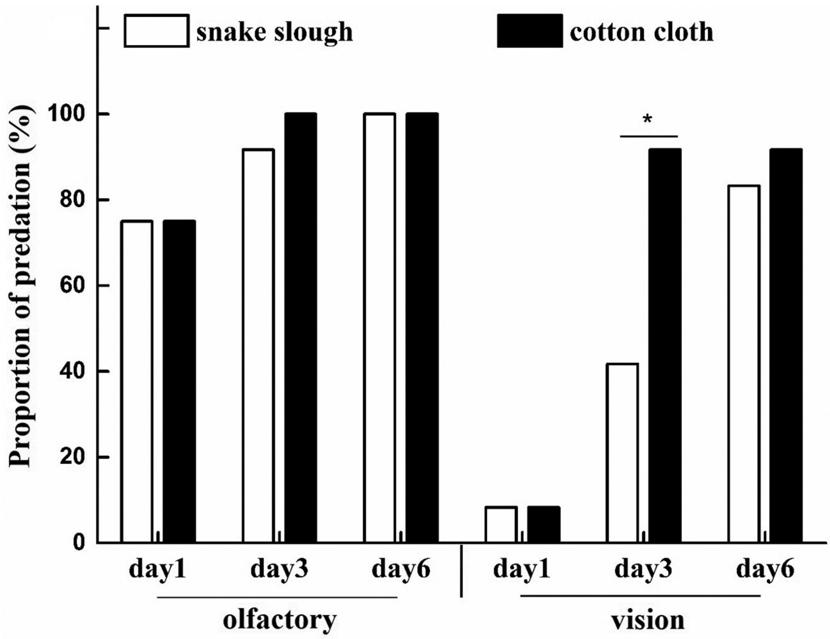

Fig. 3. — Variation in nest predation rates with snake slough odor and visibility (* refers to significant differences between the two groups).

DISCUSSION

Our results showed that the Swinhoe's striped squirrel is an egg predator of cavity-nesting birds in the study area. In the anti-predatory experiment, the predation rate of the snake slough group was lower than that of the cloth strip group, and the predation rate at which the squirrels first arrived the nest box was significantly lower in the snake slough group than in the cloth strip group, which indicates that myna and other species may have evolved the behavior of using snake slough as a nest material to reduce the risk of nest predation. In addition, this study showed that when snake slough was added to the nest it deterred nest predators mainly through its visual effects. The length of the snake slough had no significant effect on the predation rate. The fact that birds use snake slough as a nest material has been recorded as early as the end of the nineteenth century and the beginning of the twentieth century (Bolles 1890; Strecker 1926, 1927; Suthard 1927) and seems to be a common phenomenon as it has been reported in other regions (Almeida et al. 2014). Our results confirmed the speculation of early scientists and provided strong experimental evidence for the anti-predator hypothesis that snake sloughs in birds' nests may deter predators.

Alfréd and Prokop (2011) added cloth strips and snake sloughs to the nests of great reed warblers *Acrocephalus arundinaceus* (an open-nesting passerine) and found that there was no difference in the predation rate of eggs between the two groups. Therefore, they concluded that snake sloughs in the nests do not have anti-predatory effects, but instead act as a signal of the parent quality traits. However, they did not

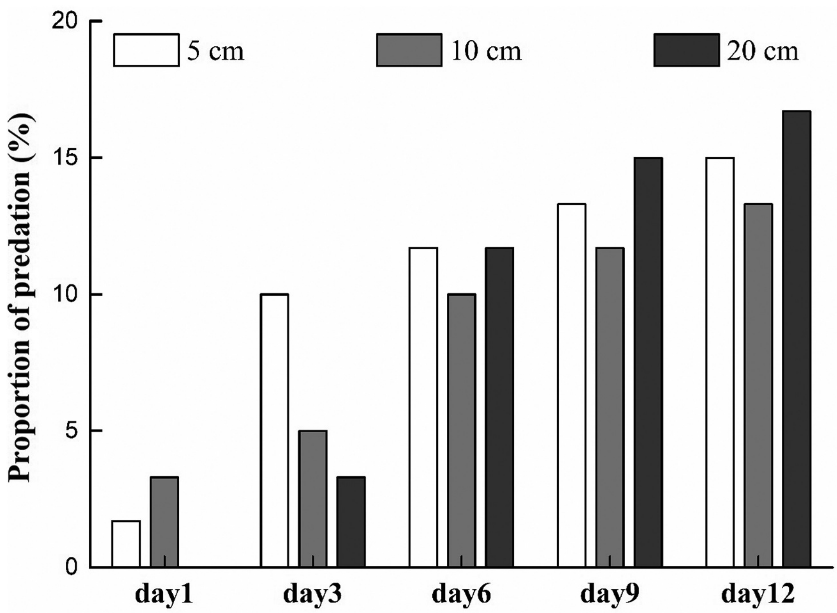

Fig. 4. — Variation in nest predation rates according to the length of the added snake slough.

completely rule out the nest predator deterrence hypothesis owing to the limitations of the experimental design and experimental time. Compared to the open nest, the use of sloughs in nest boxes makes more sense, because from a predator's perspective, sticking your head into a box that smells or looks like a snake might be dangerous. Medlin and Risch (2006) demonstrated that snake slough in nest boxes of great crested flycatchers *Myiarchus crinitus* can deter mammalian predators, especially the southern flying squirrel. Similarly, our anti-predatory experiment showed that the egg predation rate in nest boxes with snake slough was significantly lower than in nest boxes with gray cotton cloth strip, and the latency by squirrels in the experimental group was significantly longer than in the control group. These results support the anti-predation hypothesis and indicate that when snake slough is added to nest boxes it can deter nest predators. Certainly, snake sloughs in birds' nests may have other functions, such as reducing the number of parasites or pathogens in the nest and attracting potential mates. Future work should test these possibilities and examine other snake slough functions in birds' nests according to the general recommendations of experimental design (Hurlbert 1984).

Studies have shown that small mammals can respond to predators' odors (Jędrzejewski et al. 1993; Pusenius & Ostfeld 2000; Fendt 2006), especially burrowing rodents that are active during night-time or have limited visual ability (Apfelbach et al. 2005). For example, Cape ground squirrels (*Xerus inauris*) have a tendency to avoid the odor of their predators, the black-backed jackals (*Canis mesomelas*) (Belton et al. 2007); they can also distinguish between the odor of venomous and non-venomous snakes and reduce the time they stay near the source of the snake odor (Phillips & Waterman 2013). Southern flying squirrels can use odor to assess the predation risk before choosing a habitat and avoid entering nest boxes with the odor of snakes (Borgo et al. 2006). However, our experimental results showed that Swinhoe's striped squirrels recognized the snake slough in the nest box mainly by vision and the effect of the slough's odor was not important. Nevertheless, we cannot deny that the scent of snake slough may be able to deter Swinhoe's striped squirrels, as they are mainly active in daytime. Rodents active in daytime are less dependent on olfactory cues because they can use visual cues to detect predators (Clutton-Brock 1999; Waterman & Roth 2007; Edwards & Waterman 2011). Banks (1998) reported that the strongest response occurs when the target species and the odor of the predator are from the same region. The snake sloughs used in the experiment were purchased from the farm, not from the study area, thus the sloughs' odor may not have a strong impact on Swinhoe's striped squirrels in this experiment. In addition, when testing whether the rodents recognize predators through their odor, it is more common to use the predators' fresh stool and urine, which have not yet been exposed to sunlight or been dried by air (Belton et al. 2007). However, we used a small amount of air-dried snake sloughs, thus their smell was relatively weak, which may explain the insignificant effect of slough odor on Swinhoe's striped squirrels. In future experiments, fresh snake sloughs from the same region should be used to further verify the effect of the odor of snake sloughs in birds' nests on predators.

In conclusion, our study suggests that the snake sloughs in bird nests can effectively deter nest predators (e.g., Swinhoe's striped squirrels), mainly via visual effect, and the length of snake slough has no significant effect on the predation rate. Our study provides strong experimental evidence for the hypothesis that snake slough in birds' nests acts as a nest predator deterrent.

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DISCLOSURE STATEMENT

The authors declare that they have no competing interests.

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ETHICAL STANDARD

The experiments reported here comply with the current laws of China. Fieldwork was carried out without specific permit. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2016-004).

AUTHOR CONTRIBUTION

W. Liang designed the study; J. Liu carried out field experiments, performed laboratory and statistical analyses, and wrote the draft manuscript. W. Liang revised and improved the manuscript. All authors approved the final submission.

SUPPLEMENTAL DATA

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