RAFFLES BULLETIN OF ZOOLOGY **68**: 803–809
Date of publication: 30 October 2020
DOI: 10.26107/RBZ-2020-0091
http://zoobank.org/urn:lsid:zoobank.org:pub:7DEC3A7B-EB44-475F-9783-34A77B9DAF1B

Predation behaviour of the bridle snake (*Lycodon* cf. *davisonii*) on Asian tropical evergreen forest bird nests

Daphawan Khamcha* & George A. Gale

Abstract. Nest predators are responsible for the majority of reproductive failures in birds in multiple habitats globally. Snakes are likely one of the main nest predators, but few studies have focused on snake nest predation patterns in the tropics where the diversity of snakes and nesting birds is highest. Here we examined nest predation patterns of the bridle snake (*Lycodon* cf. *davisonii*), a poorly known species, but potentially a major nest predator of understorey nesting birds in Asian tropical evergreen forests. In an ongoing, long-term study of nest survival in a dry evergreen forest in northern Thailand, we monitored 478 natural nests of 23 bird species during breeding seasons of 2013–2019 with video cameras placed near active nests to assess nest predator species and their predation activities. We documented 308 predation events from 15 species of nest predators. Bridle snake was the third most important nest predator accounting for 13% of all predation events; it was exclusively nocturnal and preyed solely on eggs. Bridle snakes, unlike the other four top nest predators in our system, which were likely generalists, appeared to prefer open-cavity nests relative to other nest types, and was responsible for > 45% of nest failures of open-cavity nesting birds. This preference of the bridle snake is likely to influence nest survival rates of open-cavity nesting birds. Thus, further study of the factors influencing its predation behaviours and activity patterns, particularly its response to human disturbance, could be useful for the management of tropical forest birds.

Key words. nest predation, nest predators, open-cavity nests, tropical birds

INTRODUCTION

The use of video cameras to monitor both real and artificial nests has increased over the past two decades (Gill et al., 2016), allowing for identification of nest predators and revealing many interesting interactions between predators and nesting birds (Pierce & Pobprasert, 2007; Cox et al., 2012a; DeGregorio et al., 2014; Khamcha et al., 2018). In particular, these studies have discovered that snakes are major nest predators of forest birds. In New World temperate regions, there have been several studies which have focused on snake nest predators such as ratsnakes (*Pantherophis alleghaniensis* and *P. obsoletus*), black racer (*Coluber constrictor*), and corn snakes (*Pantherophis guttatua*) (Weatherhead et al., 2010; DeGregorio et al., 2015a; DeGregorio et al., 2016a, b). Despite snakes playing a major role in nest predation in temperate regions, they have received less attention in the tropics (Robinson et al., 2005; Koenig et al., 2007), with very few studies describing tropical snake ecology and nest predation behaviours (Khamcha et al., 2018). In tropical evergreen forests in north-eastern Thailand, snakes accounted for ~22–30% of all predation events, especially green cat snakes (*Boiga cyanea*) (Khamcha et al., 2018; Pierce et al., 2019). In a small study in Panama (Barro Colorado Island), eight of the 10 predation events recorded on video were by one species of snake (*Pseustes poecilonotus*) (Robinson et al., 2005).

More broadly, studies have shown that nest predation by snakes varies seasonally (DeGregorio et al., 2016a; Khamcha et al., 2018) and often occurs near the forest edge or in open/shrub habitats more than in the forest interior (Blouin-Demers & Weatherhead, 2001; DeGregorio et al., 2014). These patterns suggest that human disturbance and edge effects could be driving local bird extinctions through increased predation by snakes (Lahti, 2001). Temporal variation in foraging intensity was also observed (Carter et al., 2007; DeGregorio et al., 2016b; Khamcha et al., 2018). Snakes prey upon various nest species and types (Thomson & Burhans, 2004; Robinson, et al., 2005), but open-cavity nests (in shallow tree cavities) seem to be favoured by snakes in the tropical evergreen forest habitats in north-eastern Thailand (Khamcha et al., 2018). This predator-specific preference of nest type might have substantial influence on nest survival rates of open-cavity nesting birds.

Although still limited, nest predation behaviour of green cat snake has been better documented than other snake nest predators in Asian tropical forests (Pierce & Pobprasert, 2013; Khamcha et al., 2018; Somsiri et al., 2019; D'souza et al., in preparation). However, the bridle snake (*Lycodon* cf. *davisonii*) is potentially also a major nest predator in tropical

Accepted by: Evan S.H. Quah

Conservation Ecology Program, King Mongkut's University of Technology Thonburi, Bangkok, 10150, Thailand; Email: daphawan@gmail.com (*corresponding author)

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

evergreen forests in north-eastern Thailand (Khamcha et al., 2018), although its predation patterns are yet unknown. The bridle snake is extremely slender, small (total length = 794 mm, snout vent length = 598 mm, tail length = 131 mm, head depth = 4.89 mm, head width = 8.5 mm) and semi-arboreal (Das, 2010; Chan-ard et al., 2015).

We used data from an intensive, long-term video camera monitoring study of active bird nests to assess the predation behaviour of the bridle snake for seven breeding seasons in a dry evergreen forest at the Sakaerat Environmental Research Station, north-eastern Thailand. We aimed to (1) document the behaviour of the bridle snake at bird nests, (2) assess seasonal patterns in nest predation, (3) determine if nest predation by the bridle snake is affected by forest edges similar to the green cat snake, which had lower predation rates near the edge (Khamcha et al., 2018), or positively associated with edges as seen in the temperate zone (Cox et al., 2012b). In this study, we were unable to confidently identify to species level the bridle snakes from the recorded footage because of the resolution of the cameras and the necessary distance between camera and nest used to avoid potential disturbance to nesting birds, and to reduce the risk of attracting potential predators. There are two possible species of bridle snakes in our study area (C. T. Strine, pers. obs.); Blanford's bridle snake (*Lycodon davisonii*) and Malayan bridle snake (*Lycodon subannulatus*) (Cox et al., 1998, Das, 2010; Chan-ard et al., 2015). However, only the Blanford's bridle snake is confirmed to be present and frequently observed in our study area (C. T. Strine, pers. obs.). It is unclear as to whether Malayan bridle snake is also present (C. T. Strine, pers. obs.). If Malayan bridle snakes do occur in our study area, they are probably very rare based on its known distribution (Cox et al., 1998; Das, 2010; Chan-ard et al., 2015). Therefore, in this study we identified the bridle snakes observed depredating nests, as *Lycodon* cf. *davisonii*. Based on a previous study in the same study area (Khamcha et al., 2018), we hypothesised that predation patterns of bridle snake would vary seasonally and respond to forest edge similarly to green cat snake. We predicted that (1) predation rates of bridle snake would increase during periods of higher rainfall (Marques et al., 2001; Leynaud et al., 2008) and, (2) nest predation by bridle snake would be negatively associated with proximity to forest edge. We further evaluated whether bridle snake had different predation rates in relation to nest types (e.g., open cup, cavity, etc. [see below]). Given the results of our previous study (Khamcha et al., 2018), we predicted bridle snake would be responsible for a higher proportion of predation on open-cavity nests than on other nest types compared to other non-snake nest predators.

MATERIAL AND METHODS

Study area. This study was conducted in a UNESCO Biosphere Reserve, Sakaerat Environmental Research Station which is a part of the Phuluang Non-hunting area covering 160 km^2, located in north-eastern Thailand (14°30′N, 101°55′E). The dry season occurs from November to April (average rainfall 250 mm) and the wet season from May to October (average rainfall 920 mm). The average annual rainfall is 1,200 mm with peaks in May and September. The average temperature is 27°C (ranging from 19 to 36°C). Sakaerat Environmental Research Station is a forest fragment surrounded by a 5-lane highway (Route 304) to the south, villages and mono-agricultural land to the east and west, and the northern edge is attached to a reservoir created by the Lam Phra Phloeng Dam. Sakaerat Environmental Research Station was established in 1967 but was disturbed by the expansion of agriculture, which eventually led to the conversion of forest habitats to human settlements, agriculture, and grasslands. In 1982 a reforestation programme was initiated using native and exotic plants to recover degraded areas (Kamo et al., 2002). Our study area was within a section of native dry evergreen forest which makes up 70% of Sakaerat Environmental Research Station, with an elevation of 355 to 580 m asl within 1.3 kilometres of the forest edge adjacent to the highway. We collected data within two 1,000 × 200 m belt-transects separated from each other by 500 m and located perpendicular to the forest edge, and also within a 36-ha permanent research plot located between the two belt-transects, 450–1,300 m from the forest edge (Khamcha et al., 2018).

Nest monitoring and nest predator identification. During the breeding season from late January to late August we located and monitored active nests of multiple species of understorey birds. We systematically searched or intensively followed individuals or groups using behavioural cues within a 36-ha permanent research plot during the breeding seasons of 2013–2019, and within the two 1,000 × 200 m belt-transects during the breeding seasons of 2014–2016. For all nests found, we recorded species, location, distance from forest-highway edge, nest type [open cup (a cup-shaped nest placed on a simple branch or in crossings of branches, bushes, or saplings), dome (a ball-like structure constructed of vegetation with a side entrance), platform (a flat nest made of twigs layered together), closed cavity (deep cavities in which the adult bird is not visible, typical for woodpeckers and barbets) and open cavity (shallow cavities usually in a rotten stump, tree, or branch in which the adult bird is at least partly visible) (descriptions follow Pierce et al., 2019)], height above the ground, and nest stage (egg versus nestling). We set up generic waterproof infrared security video cameras on as many active (containing at least one egg to avoid nest abandonment) nests as possible. The cameras were used mainly on focal species common to our study area that build nests on the ground or in the understorey, primarily Abbott's babbler (*Malacocincla abbotti*), black-naped monarch (*Hypothymis azurea*), Indochinese blue-flycatcher (*Cyornis sumatrensis*), puff-throated babbler (*Pellorneum ruficeps*), puff-throated bulbul (*Alophoixus pallidus*), scaly-crowned babbler (*Malacopteron cinereum*), stripe-throated bulbul (*Pycnonotus finlaysoni*), and white-rumped shama (*Kittacincla malabarica*). Cameras monitored all activities at nests 24 h/day (see Khamcha et al., 2018 for additional details of video camera set-up). We restricted the height of our nest monitoring to nests approximately 0–8 m from the ground which could be reliably video-monitored (Pierce &

Pobprasert, 2007; Pierce & Pobprasert, 2013). We tended to cameras every two days in order to determine nest outcomes. We left cameras at the nests until nest fates (success or failure) were confirmed. We identified successful nests directly from the recorded footage or the presence of at least one fledgling around the nest-site. We also identified unsuccessful nests and causes of failure from recorded footage and evidence left around the nest such as eggshells, destroyed nest remains, and missing eggs/nestlings prior to the earliest possible fledgling age.

Nest predators were identified directly from the recorded footage. We recorded the actual time and duration of predation, starting when predator was visible to the camera until the predator left the view of the camera. We also recorded the frequency that each nest predator species depredated nests.

Data analysis. To assess whether nest predation by bridle snake varies seasonally and to assess the rate of nest predation by bridle snake in relation to distance from forest edge, we used generalised linear models (GLMs). The response variable was the proportion of predation events (based on number of cameras) attributed to bridle snake. We modelled the proportion of predation events using a binomial distribution. Independent variables were distance to edge (measured using a GPS) and total monthly rainfall collected from five weather stations located within a 2-km radius of the study area. We excluded temperature from the analysis. Even though temperature is expected to influence nest predator activity (Bennett, 1990), in our study area, especially during the breeding season, temperature variation was relatively small and there was no relationship between rainfall and temperature (D. Khamcha, unpublished data). We considered the evidence of variable influence on the proportion of predation events of bridle snake using 85% confidence intervals (Arnold, 2010). The statistical analysis was carried out using Program R version 3.6.0 (R Development Core Team, 2019).

RESULTS

Nest monitoring and nest predator identification. We deployed cameras at 478 natural nests of 23 species of birds. More than 90% of monitored nests (439 nests) were those of the eight focal species whose nests could be relatively easily found and monitored including Abbott's babbler (26 nests), black-naped monarch (35 nests), Indochinese blue-flycatcher (42 nests), puff-throated babbler (70 nests), puff-throated bulbul (38 nests), scaly-crowned babbler (128 nests), stripe-throated bulbul (25 nests), and white-rumped shama (75 nests). We documented 308 predation events by 15 nest predator species (Table 1), 42 predation events by unknown predators (cameras failed to detect predators), 42 events of non-predation failures (e.g., abandonment by the adults, nest damage during storms), and 86 nest successes. Of those 308 predation events, we found that bridle snake (Fig. 1) was the third most important nest predator in our study area accounting for 13% (41 predation events) of all predation events. Northern pig-tailed macaque (*Macaca leonina*) was the primary nest predator, accounting for 34% (105 events) of all predation events, followed by green cat snake accounting for 21% (64 events), common green magpie (*Cissa chinensis*) accounting for 9% (28 events), crested goshawk (*Accipiter trivirgratus*) accounting for 8% (26 events), and 10 other species accounting for the remaining 15% (44 events) of the predation events (Table 1). Nest predation by bridle snake had never been recorded during a previous intensive 3-year study in a nearby old-growth evergreen forest at Khao Yai National Park (Pierce & Pobprasert, 2013) using a similar video camera monitoring system nor had it been documented elsewhere as far as we are aware.

Fig. 1. A photograph of a bridle snake (*Lycodon* cf. *davisonii*) having just consumed a bird's egg on 27 June 2019 at 2358 at the Sakaerat Environmental Research Station, north-eastern Thailand (photo by J. Goodyear).

Predatory behaviour of bridle snake (*Lycodon* cf. *davisonii*). From seven studied breeding seasons (2013–2019), the first ever record of nest predation by bridle snake in our study area was in May 2014. Nest predations by bridle snake were recorded between 15 May and 22 June in 2014, 28 March and 3 July in 2015, 12 May and 8 July in 2016, 28 March and 29 May in 2017, 10 April and 28 June in 2018, and 20 May and 16 July in 2019. For comparison, the earliest record of predation by a green cat snake was 13 February and the latest record was 16 August. No bridle snake predation was observed in 2013 probably due to the small sample size (24 camera-monitored nests). Bridle snakes depredated solely on eggs by swallowing them whole (n = 32) or making a hole before eating all the egg contents except the shell (n = 9), while other snake nest predators in our study area, green cat snake and grey cat snake (*Boiga siamensis*), consumed both eggs and nestlings. However, because of the focal length of the cameras and nest visibility, we were unable to see the details of how the bridle snakes consumed or pierced the eggs. Bridle snakes were almost exclusively a nocturnal nest predator, with 40 out of 41 predation events occurring between 1903 and 0429 hours (first visible to the camera); there was only one predation event that occurred before sunset (1711 hours). The average nest visit by bridle snake lasted 81 min ± 10.92 (mean ±

Table 1. Nest predators and number of predation events recorded from video cameras set up at natural nests of 23 species of birds at the Sakaerat Environmental Research Station, Thailand, from 2013 to 2019.

Nest predator		***N* predation events**
Snakes		**108**
Green cat snake	*Boiga cyanea*	64
Grey cat snake	*Boiga siamensis*	3
Bridle snake	*Lycodon* cf. *davisonii*	41
Birds		**61**
Common green magpie	*Cissa chinensis*	28
Crested goshawk	*Accipiter trivirgratus*	26
Shikra	*Accipiter badius*	3
Asian barred owlet	*Glaucidium cuculoides*	3
Unidentified raptor[a]	*Accipiter* sp.	1
Mammals		**138**
Northern pig-tailed macaque	*Macaca leonina*	105
Common palm civet	*Paradoxurus hermaphroditus*	7
Grey-bellied squirrel	*Callosciurus caniceps*	12
Variable squirrel	*Callosciurus finlaysonii*	2
Northern treeshrew	*Tupaia belangeri*	6
Rat/*Maxomys*[b]	–	5
Indochinese ground squirrel	*Menetes berdmorei*	1
Arthropods		**1**
Centipede	*Scolopendra* sp.	1
Total		308

[a]Unidentified raptor, either crested goshawk (*Accipiter trivirgratus*) or shikra (*Accipiter badius*)
[b]Unable to identify to species from recorded footage.

Table 2. Number of nests of the observed bird species depredated by bridle snakes (*Lycodon* cf. *davisonii*) during 6 breeding seasons (2014 to 2019) in Sakaerat Environmental Research Station, Thailand.

No	**Species**	***N***	**Avg. nest height (m)**	**Nest type**
1	Abbott's babbler *Malacocincla abbotti*	2	0.7	open cup
2	Puff-throated bulbul *Alophoixus pallidus*	3	1.7	open cup
3	Scaly-crowned babbler *Malacopteron cinereum*	1	1.5	open cup
4	Stripe-throated bulbul *Pycnonotus finlaysoni*	3	1.2	open cup
5	Indochinese blue-flycatcher *Cyornis sumatrensis*	7	0.6	open cavity
6	White-rumped shama *Kittacincla malabarica*	25	1.6	open cavity
	Total	41		

Note: Open cavity is a shallow cavity usually in a rotten stump, tree, or branch in which the adult bird is at least partly visible.

SE). Duration of nest visits by bridle snake at open-cavity nests (81 min ± 13.27) was similar to that of open-cup nests (79 min ± 9.80).

From a total of 308 predation events, 287 predation events (93%) were recorded at the nests of eight focal species. We documented 41 predation events by bridle snake on six out of the eight focal species, including species with open-cavity nests and open-cup nests (Table 2). Our data indicated that bridle snakes preyed more on open-cavity nests (chi square = 35.017, $p < 0.001$) than on open-cup nests, especially white-rumped shamas, with their nests depredated more by bridle snake than expected by chance (chi square = 32.847, $p < 0.001$) (Fig. 2). In contrast, northern pig-tailed macaque was more likely to prey on open-cup nests (chi square = 114.97, $p < 0.001$). Green cat snake, the second most important predator in our study site, did not demonstrate a preference for nest type (chi square = 1.145, $p = 0.564$) (Fig. 2). The average height of the nests bridle snake depredated was 1.2 m (range 0.3–4 m). We never recorded a bridle snake

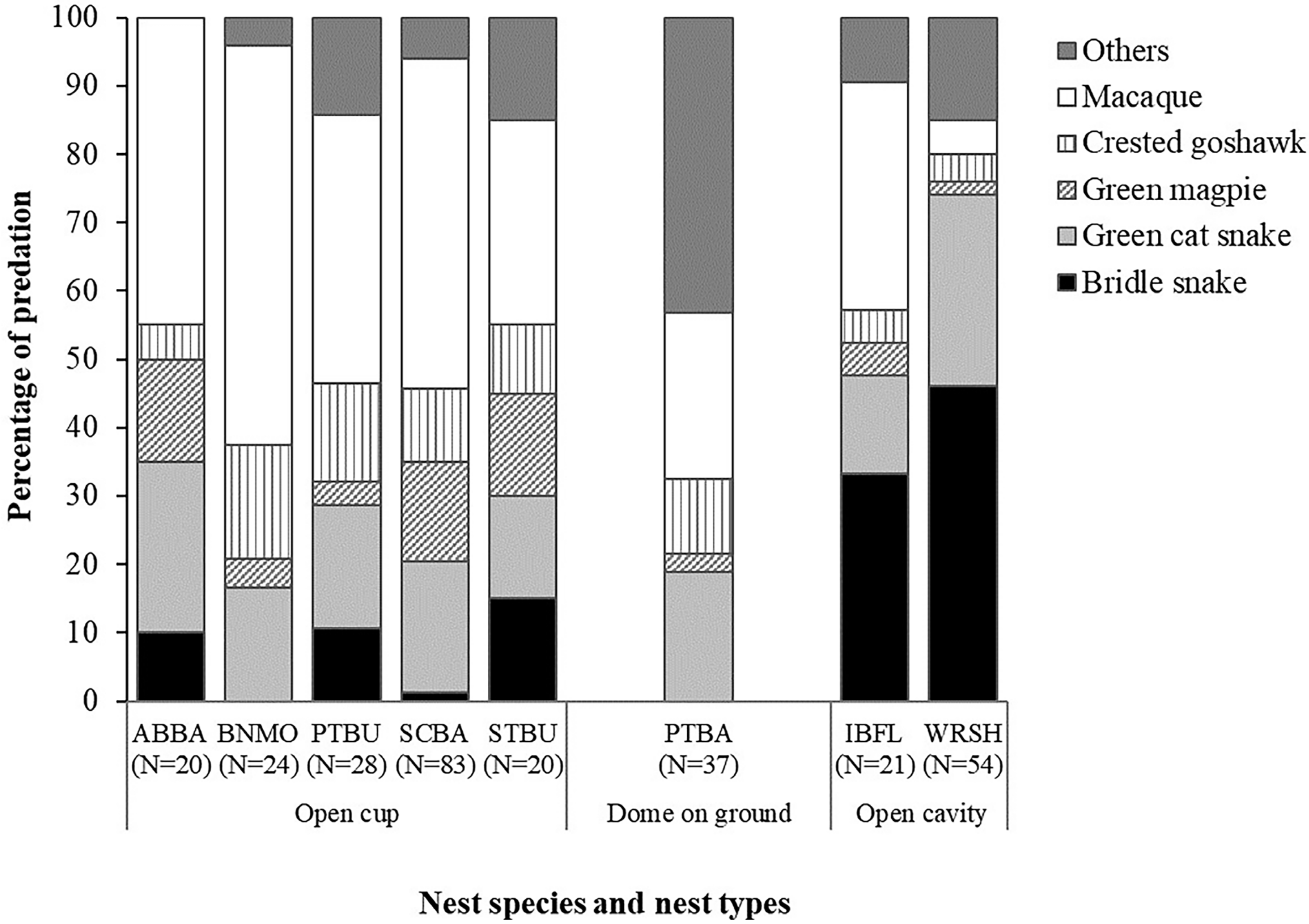

Fig. 2. Percentage of depredated nests for eight focal species caused by the top five nest predators at the Sakaerat Environmental Research Station, Thailand during the 2013–2019 breeding seasons. ABBA = Abbott's babbler, BNMO = black-naped monarch, IBFL = Indochinese blue-flycatcher, PTBA = puff-throated babbler, PTBU = puff-throated bulbul, SCBA = scaly-crowned babbler, STBU = stripe-throated bulbul, WRSH = white-rumped shama. N represents number of observed predation events for each nesting species.

predation event on a ground nest although only 12% of the depredated nests were located on the ground (Fig. 2).

We found no seasonal pattern of nest predation by bridle snake and there was no evidence that rainfall influenced predation by bridle snake ($\beta = 0.003$; 85% CI = -0.0003 to 0.0064). We also found no evidence to suggest there was an effect of distance to forest edge on predation by bridle snake ($\beta = 0.001$; 85% CI = -0.00003 to 0.002).

DISCUSSION

Bridle snake was a major nest predator (accounting for 13% of all predation events) in our study area at Sakaerat Environmental Research Station over six breeding seasons (2014–2019). It was responsible for 46% of nest failures of open-cavity nesters (white-rumped shama and Indochinese blue-flycatcher). It appears to be an exclusively nocturnal nest predator and egg eater. We found no support for the influence of rainfall or distance to forest edge on nest predation by bridle snake.

Previous studies suggested that snake nest predators tended to depredate nestlings rather than eggs (Benson et al., 2010; DeGregorio et al., 2016b). At Sakaerat Environmental Research Station, however, bridle snake was solely an egg hunter. Based on their small-body size, depredation on eggs may reduce the risk of being injured by parent bird defences which typically increase with the age of the nestling (Montgomerie & Weatherhead, 1988), although nocturnal predation is likely to allow nest predators to avoid nest defences of adult birds (Ellison & Ribic, 2012).

In contrast to green cat snakes, we found no significant differences in predation rates by bridle snake in response to seasonal changes in rainfall. As reported in Khamcha et al. (2018), nest predation events of green cat snake increased with increasing rainfall, possibly due to greater activity levels of green cat snake during higher rainfall periods. However, some reports have found no relationship between activity levels of snakes and rainfall (Daltry et al., 1998; Brown & Shine, 2002). The influence of environmental factors on movement and activity patterns of snakes are obscure especially in tropical regions simply due to the difficult nature of surveying for snakes (Eskew & Todd, 2017). Many studies have documented relatively higher nest predation by snakes closer to forest edges (Cox et al., 2012b; DeGregorio et al., 2014). Our study of nest predation by multiple species at Sakaerat Environmental Research Station in Khamcha et al. (2018), however, found that the responses to the forest edge by nest predators were species-specific. We found no response to the forest edge regarding nest predation by bridle snake, possibly because bridle snake is a forest generalist occurring in a wide range of forest types (both forest interior and forest edges) and also range from lowland to montane habitats (Das, 2010; Ecology Asia, 2019). In contrast, nest predation by green cat snake in our study was greater in the forest interior, which may be due to their avoidance of edge habitat (Khamcha et al., 2018). Furthermore, Khamcha et al. (2018) found that the number of detections of bridle snakes from 37 night line transect surveys (3 detections at the edge vs. 5 detections at the interior) and 750 snake trap-nights using drift fence traps (1 detection at the edge vs. 1 detection at the interior) were not different between edge and forest interior habitats, although the number of detections was very small.

We found support for our hypothesis that predation patterns of bridle snake varied among different nest types. Bridle snakes appeared to more frequently prey on open-cavity nests, especially those of white-rumped shamas, relative to open-cup nests and we observed no predation events by bridle snake on ground nests. This pattern was similar to other studies where snake predation is an important determinant of nest failure for cavity nesting birds (Neal et al., 1993; Koenig et al., 2007). During six breeding seasons we never recorded nests depredated by bridle snake before 28 March, which may have corresponded to the breeding period of white-rumped shamas, their apparent focal nesting prey, which mostly started nesting after mid-March (Chotprasertkoon et al., 2017; Angkaew et al., 2019).

The preference for open-cavity nests by bridle snake could be due to their behaviour. Being semi-arboreal, bridle snakes commonly move through connected vegetation and tree trunks, and sometimes shelter in tree cavities and perhaps search for prey in these areas (Brightsmith, 2005).

High predation rates on open-cavity nests by bridle snake are probably having substantial effects on nest survival rates of open-cavity nesting birds in our study area. Thus, changes in bridle snake behaviours, activities or abundances caused directly or indirectly by abiotic or biotic factors (e.g., climate, vegetation structure, etc.), particularly in previously disturbed habitat like Sakaerat Environmental Research Station, may have important consequences not only for breeding performance but also for population dynamics of their prey (Sperry et al., 2008; Cox et al., 2013; DeGregorio et al., 2015b).

CONCLUSIONS

Our results indicated that the bridle snake is one of the main predators in this dry evergreen forest of north-eastern Thailand. We found unique predation behaviours; it appeared to have a preference for open-cavity nests and was almost exclusively a nocturnal nest predator. Moreover, the bridle snake depredated solely on eggs by swallowing them whole or interestingly, sometimes puncturing the eggs before eating the entire contents except the shell. Our findings suggest that further studies on bridle snake behaviour and activity patterns would be useful for predicting long-term impacts on forest birds along with studies of other tropical snake nest predators, e.g., green cat snake in this region or others such as the Neotropical bird snake (*Pseustes poecilonotus*). Our study and others indicate that snakes are major nest predators in almost every habitat and every region globally. Thus, it is important to understand their predation behaviours and activity patterns and how these might impact ecosystem function (Weatherhead & Blouin-Demers, 2004). Additionally, understanding which mechanisms (e.g., vegetation structure, climate, human activity, and interactions among nest predators) have an influence on their foraging behaviour and activity patterns, would offer significant advancement in our knowledge of the population dynamics of bird communities.

ACKNOWLEDGEMENTS

We thank T. Artchawakom and S. Waengsothorn, the former and current directors of Sakaerat Environmental Research Station for permission to conduct this study. We are grateful to A. Pierce, W. Sankamethawee, R. Angkaew, P. Doungkomna, K. Somsiri, M. Pringprao, former and current research assistants of the Sakaerat bird team and interns who provided extensive logistical support and found many, many nests. Thanks also to C. Strine for valuable comments on an earlier draft of this paper. We also thank D. Ngoprasert for his advice on the statistical analysis. This research was funded by King Mongkut's University of Technology Thonburi (Thailand) (grant number 58 000 312), the National Research Council of Thailand (grant numbers 59 000 190 and 60 000 088), and the National Science and Technology Development Agency (grant numbers CPMO P-13-00367 and CPMO P-14-51347). DK was supported by the Royal Golden Jubilee Ph.D. Program, Thailand (grant number PHD/0036/2556). Finally, special thanks to E. Quah (associate editor), P. Weatherhead, and one anonymous reviewer for their useful comments.

LITERATURE CITED

Angkaew R, Sankamethawee W, Pierce AJ, Savini T & Gale GA (2019) Nesting near road edges improves nest success and post-fledging survival of White-rumped Shamas (*Copsychus malabaricus*) in northeastern Thailand. Condor, 121: 1–15.

Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management, 74: 1175–1178.

Bennett AF (1990) Thermal dependence of locomotor capacity. American Journal of Physiology, 259: R253–R258.

Benson TJ, Brown JD & Bednarz JC (2010) Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology, 79: 225–234.

Blouin-Demers G & Weatherhead PJ (2001) Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology, 82: 3025–3043.

Brightsmith DJ (2005) Competition, predation and nest niche shifts among tropical cavity nesters: ecological evidence. Journal of Avian Biology, 36: 74–83.
Brown GP & Shine R (2002) Influence of weather conditions on activity of tropical snakes. Austral Ecology, 27: 596–605.
Carter GM, Legare ML, Breininger DR & Oddy DM (2007) Nocturnal nest predation: a potential obstacle to recovery of a Florida Scrub-jay population. Journal of Field Ornithology, 78: 390–394.
Chan-ard T, Parr JWK & Nabhitabhata J (2015) A Field Guide to the Reptiles of Thailand. Oxford University Press, New York, 352 pp.
Chotprasertkoon T, Pierce AJ, Savini T, Round PD, Sankamethawee W & Gale GA (2017) Influence of vegetation cover on nest cavity selection and nesting success of White-rumped Shamas (*Copsychus malabaricus*): an experimental test. Wilson Journal of Ornithology, 129: 727–741.
Cox MJ, Van Dijk PP, Nabhitabhata J & Thirakhupt K (1998) A Photographic Guide to Snakes and Other Reptiles of Peninsular Malaysia, Singapore and Thailand. New Holland Publishers, London, 144 pp.
Cox WA, Pruett MS, Benson TJ, Chiavacci SJ & Thompson FR III (2012a) Development of camera technology for monitoring nests. In: Ribic CA, Thompson FR III & Pietz PJ (eds.) Video surveillance of nesting birds. Studies in Avian Biology. No 43. University of California Press, Berkeley. Pp. 185–210.
Cox WA, Thompson FR III & Faaborg J (2012b) Landscape forest cover and edge efects on songbird nest predation vary by nest predator. Landscape Ecology, 27: 659–669.
Cox WA, Thompson FR II & Riedy JL (2013) The efects of temperature on nest predation by mammals, birds and snakes. The Auk, 130: 1–7.
Daltry JC, Ross T, Thorpe RS & Wuster W (1998) Evidence that humidity influences snake activity patterns: a field study of the Malayan pit viper *Calloselasma rhodostoma*. Ecography, 21: 25–34.
Das I (2010) A Field Guide to the Reptiles of Thailand & South-east Asia. Asia Books Co., Ltd, Bangkok, 376 pp.
DeGregorio BA, Sperry JH & Weatherhead PJ (2015a) Wait until dark? Daily activity patterns and nest predation by snakes. Ethology, 121: 1–10.
DeGregorio BA, Weatherhead PJ & Sperry JH (2014) Power lines, roads, and avian nest survival: effects on predator identity and predation intensity. Ecology and Evolution, 4: 1589–1600.
DeGregorio BA, Weatherhead PJ, Ward MP & Sperry JH (2016a) Do seasonal patterns of Ratsnake (*Pantherophis obsoletus*) and Black Racer (*Coluber constrictor*) activity predict avian nest predation? Ecology and Evolution, 6: 2034–2043.
DeGregorio BA, Weatherhead PJ, Ward MP & Sperry JH (2016b) Ecology and predation behavior of Corn snakes (*Pantherophis guttatus*) on avian nests. Herpetological Conservation and Biology, 11: 150–159.
DeGregorio BA, Westervelt JD, Weatherhead PJ & Sperry JH (2015b) Indirect effect of climate change: shifts in ratsnake behavior alter intensity and timing of avian nest predation. Ecological Modelling, 312: 239–246.
Ecology Asia (2019) Snakes of South East Asia. https://www.ecologyasia.com/verts/snakes/davison's-bridle-snake.htm (Accessed on 15 July 2019).
Ellison K & Ribic CA (2012) Nest defense: grassland bird responses to snakes. In: Ribic CA, Thompson FR III & Pietz PJ (eds.) Video surveillance of nesting birds. Studies in Avian Biology. No 43. University of California Press, Berkeley. Pp. 149–159.
Eskew EA & Todd BD (2017) Too cold, too wet, too bright, or just right? Environmental predictors of snake movement and activity. Copeia, 105: 584–591.
Gill RA, Cox WA & Thompson FR (2016) Timing of songbird nest predation as revealed by video surveillance. The Wilson Journal of Ornithology, 128: 200–203.
Kamo K, Vacharangkura T, Tiyanon S, Viriyabuncha C, Nimpila S & Doangsrisen B (2002) Plant species diversity in tropical planted forests and implication for restoration of forest ecosystems in Sakaerat, Northeastern Thailand. Japan Agricultural Research Quarterly, 36: 111–118.
Khamcha D, Powell LA & Gale GA (2018) Effects of roadside edge on nest predators and nest survival of Asian tropical forest birds. Global Ecology and Conservation, 16: e00450.
Koenig SE, Wunderle J & Enkerlin-Hoeflich EC (2007) Vines and canopy contact: a route for snake predation on parrot nests. Bird Conservation International, 17: 79–91.
Lahti DC (2001) The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation, 99: 365–374.
Leynaud GC, Reati GJ & Bucher EH (2008) Annual activity patterns of snakes from central Argentina (*Cordoba province*). Studies on Neotropical Fauna and Environment, 43: 19–24.
Marques OVA, Eterovic A & Endo W (2001) Seasonal activity of snakes in the Atlantic forest in southeastern Brazil. Amphibia-Reptilia, 22: 103–111.
Montgomerie RD & Weatherhead PJ (1988) Risk and rewards of nest defence by parent birds. The Quarterly Review of Biology. 63: 167–187.
Neal JC, Montague WG & James DA (1993) Climbing by black rat snakes on cavity trees of Red-cockaded Woodpeckers. Wildlife Society Bulletin, 21: 160–165.
Pierce AJ & Pobprasert K (2007) A portable system for continuous monitoring of bird nests using digital video recorders. Journal of Field Ornithology, 78: 322–328.
Pierce AJ & Pobprasert K (2013) Nest predators of Southeast Asian evergreen forest birds identified through continuous video recording. Ibis, 155: 419–423.
Pierce AJ, Sankamethawee W, Powell LA & Gale GA (2019) Patterns of nesting and nest success in an evergreen forest in Southeast Asia. Emu-Austral Ornithology, 120: 46–55.
R Development Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (Accessed 12 June 2019).
Robinson WD, Rompre G & Robinson TR (2005) Videography of Panama bird nests shows snakes are principal predators. Ornitologia Neotropical, 16: 187–195.
Somsiri K, Gale GA, Pierce AJ, Khamcha D & Sankamethawee W (2019) Habitat structure affects nest predation of the Scaly-crowned Babbler (*Malacopteron cinereum*) by macaques and snakes in a Thai-seasonal evergreen forest. Journal of Ornithology, 161: 389–398.
Sperry JH, Peak RG, Cimprich DA & Weatherhead PJ (2008) Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology, 39: 379–383.
Thompson FR III & Burhans DE (2004) Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. Conservation Biology, 18: 373–380.
Weatherhead PJ & Blouin-Demers G (2004) Understanding avian nest predation: why ornithologists should study snakes. Journal of Avian Biology, 35: 185–190.
Weatherhead PJ, Carfagno GLF, Sperry J, Brawn, JD & Robinson SK (2010) Linking snake behavior to nest predation in a Midwestern bird community. Ecological Applications, 20: 234–241.