Identifying predators of passerine shrub and ground nests in a lowland forest of Taiwan

台灣低海拔森林燕雀目鳥類灌叢巢與地面巢的天敵判別

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Abstract

Predation is one of primary causes of nest failure for passerines. We applied an infrared time-lapse video system to continually monitor ground and shrub nests of six small passerine species in a disturbed lowland forest in central Taiwan from 2006 to 2007. The daily predation rate of shrub nests (0.059 ± 0.006) was higher than that of ground nests (0.034 ± 0.005, χ^2 = 5.84, p = 0.016). We recorded 17 species of nest predators that were classified into five predation types: snakes (8 species), birds (4 species), macaques (*Macaca cyclopsis*) (1 species), other mammals (4 species), and ants (one unidentified species). Snakes were major predators of both shrub and ground nests. Macaques preyed on shrub and ground nests equally. Avian predators were more focused on shrub than ground nests while other mammalian predators preferred ground nests. Predators such as snakes and ants left no traces but only an empty nest. Therefore, identifying these predators without video surveillance was almost impossible. Each other type of predator would leave characteristic marks that could be identified later. Raptors usually caught the parents in the nest and left the feathers on the rim of the nest while ignoring the unhatched eggs. Macaques always left a distinctive mess around the nest. Other mammalian predators would usually leave footprints and a loosened nest. We established guidelines for identifying predator types based on the marks around the preyed nests.

摘 要

天敵掠食是造成小型燕雀目鳥類繁殖失敗的主因之一。2006-2007 年繁殖期間，在中台灣一處受擾動的低海拔森林中，監測 6 種小型燕雀目鳥類的地面巢與灌叢巢，並利用紅外線縮時錄影系統持續記錄，作為輔助。其中，灌叢巢（0.059 ± 0.006）面臨的每日被掠食率高於地面巢（0.034 ± 0.005, $\chi^2 = 5.84$, $p = 0.016$）。研究期間共記錄到 17 種鳥巢掠食者，分為蛇類（8 種）、鳥類（4 種）、台灣獼猴（1 種）、其他哺乳類（4 種）以及螞蟻（不知名種）等五種掠食者類型。無論是灌叢巢或地面巢，蛇類都是最主要的天敵，台灣獼猴沒有特別偏好的巢型，鳥類天敵傾向掠食灌叢巢，而其他哺乳類天敵則偏好地面巢。大多數的蛇類和螞蟻在掠食後只會留下一個空的鳥巢，不留有其他痕跡，若沒有鳥巢的錄影資料將幾乎無法判定天敵種類，除此之外，不同類型的天敵在掠食後，會留下獨特的痕跡可供辨識。猛禽通常會將巢中的親鳥抓走，並留下親鳥的羽毛在巢的邊緣和未孵化的蛋。台灣獼猴常常在巢邊留下容易辨識的混亂痕跡。而其他哺乳類天敵通常會留有腳印並造成被掠食的鳥巢鬆落。因此，我們將被掠食的鳥巢痕跡及其周圍環境遺跡歸納出一些可供判定其天敵類型的準則。

Key words: infrared time-lapse video photography, nest fate, predator determination, predation risk, subtropical region

關鍵詞：紅外線縮時錄影系統、鳥巢命運、天敵判定、掠食風險、亞熱帶地區

收件日期：2014 年 10 月 07 日 接受日期：2015 年 03 月 26 日

Received: October 07, 2014 Accepted: March 26, 2015

Introduction

Nest predation is the primary cause of nest failure for many passerines (Ricklefs 1969; Martin 1993), and the rate of successful breeding is an important factor influencing bird populations. Identifying the causes of nest failure helps to determine factors affecting nesting success. A “nest predator” is any species that removes or damages eggs or nestlings

(Thompson III *et al.* 1999; Thompson III and Burhans 2004). To fully understand nest predation pattern, it is critical to investigate local nest predator composition and predators' densities, searching tactics and spacing behavior as well as densities of alternative preys (Hanski *et al.* 1996). And the spacing behavior means the activity pattern of predators such as macaques could climb trees while most rodents stay on the ground. Among these factors, predator identification is the first step to clarify nest predation pattern.

There were numerous studies on nest predation in temperate and tropical regions, especially in Central and South America (Wikelski *et al.* 2003; Rader *et al.* 2007; Brawn *et al.* 2011). However, only a few nest predation researches for tropical and subtropical Asia have been published, partially due to the different patterns in predator shifts among biogeographical regions and landscapes. Predation risk is related to the composition and density of predators. The nest predation risk in tropical and subtropical regions appear to be higher than the temperate region for a variety of reasons such as the diversity and density of predators may be much higher in the low latitudes, but some are still barely understood (Gibbs 1991; Martin 1996; Auer *et al.* 2007).

The studies of nest predator using artificial and real nests showed different results. A few nest predation studies in tropical Asia experimented with artificial nests (Cooper and Francis 1998; Wong *et al.* 1998; Sodhi *et al.* 2003; Pangau-Adam *et al.* 2006). In the tropical lowland forest of Singapore, artificial ground nests were found preyed by lizards, crows, squirrels, wild pigs, feral dogs, banded leaf monkeys, and long-tailed macaques with video monitoring (Wong *et al.* 1998). Rodents were the most common predators of both ground and shrub artificial nests, and the shrub nests were more susceptible to dwarf cuscus, squirrels, and tree snakes in Sulawesi (Pangau-Adam *et al.* 2006). However, a recent real nest study in Thailand found that macaques and snakes were the main predators (Pierce and Pobprasert 2013).

Because natural nests are difficult to find, working with artificial nests baited with quail and plasticine eggs is an easier way to study nest predators. Plasticine eggs often allow a clear separation of predator types (Söderström *et al.* 1998; Pangau-Adam *et al.* 2006) as some mammalian and avian predators may leave marks on these eggs, though not allowing identification to the species level. However, these artificial nests cannot simulate the whole breeding stage without incubating parents and chicks in the nest (Melville *et al.* 2014). In addition, lacking live animals to produce natural sounds and smells induces biases. For example, no snakes predate these artificial nests (Part and Wretenberg 2002; Thompson III and Burhans 2004).

To identify the nest predator to the species level is challenging. Depending on the remnants found in and around the nests, such as nest lining disruption, eggshell fragments, remains of eaten chicks left at nests, footprints around nests, predator types and species may be identified (Brown *et al.* 1998). However, these remnants also do not always allow unambiguous identification of predator type or species. Moreover, parent birds sometimes might alter the remnants after the predation event (Brown *et al.* 1998).

While direct observation would be ideal, direct human observations of nest predation events are rare and may also bias results because the presence of the human may deter potential predators. Therefore, a new technical nest monitoring system that applied time-lapse video photography was developed in recent decades to provide an effective tool to identify nest predators (Williams and Wood 2002; Renfrew and Ribic 2003; Stake and Cimprich 2003; Peterson *et al.* 2004; Stake *et al*. 2004; Sabine *et al.* 2005; Rader *et al.* 2007). This technique used on real nests is definitely the most reliable method because it helps to eliminate all the biases mentioned above and usually allows accurate species identification of the predator (Cutler and Don 1999).

In this study, we identified and compared the nest predator species or types between ground and shrub passerine nests using video photography in subtropical lowland forests of Taiwan. We linked them to the typical remnants left after the predation event and established guideline for identifying predator types. Finally, we compared the predation risk between videoed and non-videoed nests.

Methods

Study area

This study was conducted in Huben Village, Linnei Township, Yunlin County in west-central Taiwan (120˚37.1'E, 23˚44.5'N) (Fig. 1.). Huben Village was designated as an Important Bird Area (IBA) mainly for the conservation of the Fairy Pitta (*Pitta nympha*) by the Chinese Wild Bird Federation (2001) which was later endorsed by BirdLife International. The study area is about 250 ha with elevation ranging from 50 to 500 m, and more than 50 % of the area is covered by Ma Bamboo (*Dendrocalamus latiflorus* Munro). Secondary broadleaf trees are common on the sides of ravines and ridges. Orange orchards and betel nut (*Areca catechu*) plantations are sparsely distributed in the area.

Nest searching and monitoring

Nests were searched during the breeding seasons from early March until late August in 2006 and 2007 based on parental behavior cues, systematic searches, and parent flushes. Located nests were not higher than 2 m from the ground. Nests built directly on the ground were categorized as ground nests, while those built within small trees or low stems were classified as shrub nests.

Once a nest was found, we recorded the nesting stage (building, laying, incubation or nestling stage) and the coordinates using GPS (GPSMAP 60CSx, Garmin Corporation, Hsi-Chih, Taipei, Taiwan), and filled out a nest card (Martin *et al.* 1997) to describe the nest characteristics and location for later revisits.

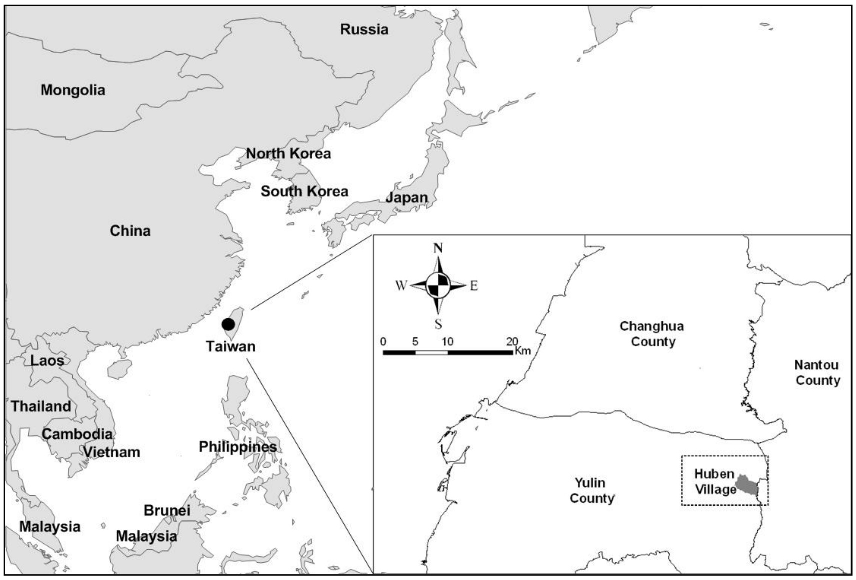


Fig. 1. Map of the Huben Village study area in west-central Taiwan.

Each nest was checked every three to four days to determine its status. When the nest appeared preyed upon (eggs or young removed), we recorded the nest structure and searched the area immediate surrounding the nest for evidence of predation, such as eggshells, bodies, animal footprints, animal route and broken nests (Martin and Geupel 1993).

Video photography and predator identification

The video system was only set on active nests that had eggs or young in the nest to record nest predators and breeding behavior. To record as much nest breeding data as possible, nests that were in the laying and incubation stages had priority. We also attempted to video ground and shrub nests equally to compare their predators.

We monitored the active nests by a time-lapse video photography system which consisted of an infrared camera with 850 nm infrared wavelength (EZ230, EverFocus Electronics Corporation, Hsi-Chih, Taipei, Taiwan), digital recorder (ESDR400H, EverFocus Electronics Corporation, Hsi-Chih, Taipei, Taiwan) and a cable powered by three rechargeable, 12-volt, deep-cycle batteries. The video system was placed in a 56×56×76 mm waterproof housing and we precluded setting the system on ravines to avoid the system being washed away in a storm. A tripod with a mounted camera was placed 1.5 m from the nest and was connected with a 50-100 m cable with the video recording system set up 20-50 m away to reduce the disturbance by human activities. The video system continuously recorded the nesting activity for 24 hours a day at a speed of 5 frames/sec. A 250 GB hard disk allowed 24-hour of monitoring for 14 days. The video photography was colored in the light and black and white in the dark. We visited the recorder and replaced the batteries every other day until the chicks fledged or the nest failed. We used a hand-held monitor to check the status of nests without approaching them directly.

If a nest was preyed upon, we reviewed the digital videos thoroughly to confirm the predators and the predation process.

Statistical analysis

Nest survival data were obtained by locating and monitoring nests following the field protocol (Martin *et al.* 1997). We also used Mayfield logistic regression modeling to estimate the daily predation rate (Aebischer 1999; Hazler 2004; Hazler 2006). Mayfield logistic regression is based on the Mayfield estimator (Mayfield 1961; 1975). We compared daily predation rates at monitored nests with and without video and tested the effect of the photographic system on nest predation rates in program CONTRAST (Hensler and Nichols 1981; Hines and Sauer 1989) which is based on establishing variance covariance matrices that contrast two or more nest survival rates and then comparing their differences with a chi-square distribution.

Results

In the breeding seasons of 2006 and 2007, we monitored 234 nests (143 shrub nests and 91 ground nests) of six species: Grey-cheeked Fulvetta (GF, *Alcippe morrisonia*), Black-naped Monarch (BM, *Hypothymis azurea*), Light-vented Bulbul (LB, *Pycnonotus sinensis*), Dusky Fulvetta (DF, *Schoeniparus brunneus*), Fairy Pitta (FP, *Pitta nympha*) and Taiwan Scimitar-Babbler (SB, *Pomatorhinus musicus*) (Table 1).

Table 1. Daily predation rates (±SD) at shrub and ground nests in Huben village from March to July 2006 and 2007

Type	No. of nests	No. of depredated nests	Observation days	Daily predation rate
Shrub nests	**143**	**93**	**1,625**	**0.062±0.006**
Grey-cheeked Fulvetta (*Alcippe morrisonia*)	110	73	1,286.5	0.061±0.007
Black-naped Monarch (*Hypothymis azurea*)	11	7	122	0.057±0.021
Light-vented Bulbul (*Pycnonotus sinensis*)	16	11	146.5	0.082±0.023
Fairy Pitta (*Pitta nympha*)	4	1	27	0.037±0.036
Dusky Fulvetta (*Schoeniparus brunneus*)	2	1	43	0.023±0.023
Ground nests	**91**	**45**	**1,343.5**	**0.038±0.005**
Fairy Pitta (*Pitta nympha*)	53	21	888.5	0.029±0.007
Dusky Fulvetta (*Schoeniparus brunneus*)	17	13	184.5	0.076±0.019
Taiwan Scimitar-Babbler (*Pomatorhinus musicus*)	21	11	270.5	0.041±0.012

Among the ground nests, 45 nests (49.5%) were preyed, and the daily predation rate was 0.038±0.005 (1,343.5 observed days). Three nests (3.3%) were destroyed by rain, one nest (1.1%) was destroyed by humans, three nests failed for unknown reasons, and 39 nests (42.9%) were successful (i.e. fledged one or more young).

For the shrub nests, 93 nests (65.0%) were preyed, and the daily predation rate was 0.062±0.006 (1,625 observed days) which was higher than the rate for ground nests ($\chi^2 = 8.89$, $p = 0.003$). Six nests (4.2%) were destroyed by rain, two nests (1.4%) were destroyed by humans, one nest (0.7%) failed due to unknown reasons, and 41 nests (28.7%) were successful.

Nest predators

We monitored 117 out of a total of 234 nests using video photography. Among them, 70 predation events were recorded that included 64 nests which each was preyed by one predator and six nests (Grey-cheeked Fulvetta (n=3), Fairy Pitta (n=2), and Light-vented Bulbul (n=1)) which each was recorded predation events twice. Of these, 44.3% (n=31) and 55.7% (n=39) were diurnal and nocturnal predators, respectively. Most snakes were nocturnal (79.6%, n=35), while macaques (08:19 to 17:33) and avian predators (06:36 to 18:00) were exclusively diurnal, and other mammals appeared in both day and night times (Fig. 2).

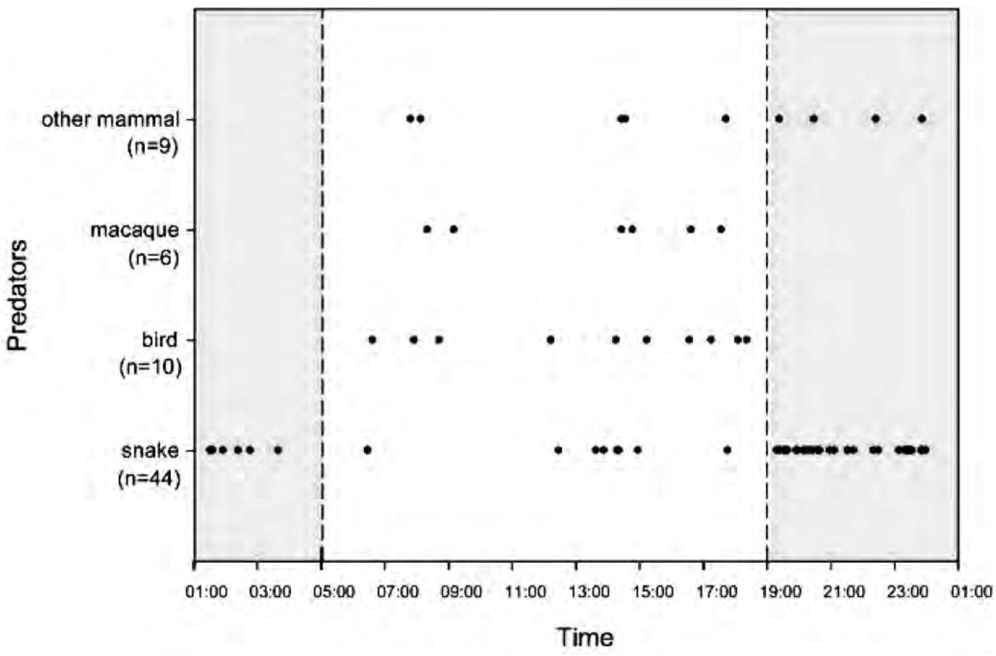


Fig. 2. Occurrence times of four predator groups visiting song bird nests in Huben Village from March to July in 2006 and 2007. We did not display the occurrence time of ants in this figure because they were too small in the video photography to identify their first predation time.

We identified eight species of snakes, four species of birds, macaques (1 species, Taiwan only) and four species of other mammals (Table 2). Macaques and other mammals were separated in two groups due to their different activity pattern. Macaques would move between ground and trees while other mammals usually stayed on the ground.

Table 2. Ground and shrub nest predators for Fairy Pitta (FP), Taiwan Scimitar-Babbler (SB), Dusky Fulvetta (DF), Light-vented Bulbul (LB), Black-naped Monarch (BM) and Grey-cheeked Fulvetta (GF) recorded by video in Huben village from March to July 2006 and 2007 during the laying, incubation, or nestling stages

Predator Type	Species	Ground nests							Shrub nests							
		Laying	Incubation			Nestling			Incubation				Nestling			
		FP	FP	SB	DF	FP	SB	DF	LB	BM	GF	FP	BM	GF	FP	DF
Snake	Tree snake															
	Boiga kraepelini		2	1	1	1			2		5		1	5		
	Ground snake															
	Oligodon formosanus			1										1		
	Ptyas mucosus		3													
	Lycodon rufozonatus					1		1								
	Elaphe carinata	1									1					1
	Psammodynastes pulverulentus					1										
	Orthriophis taeniura friesi											1		1		
	Protobothrops mucrosquamatus						1	1					1	2		
	Unidentified snake			1		1	1				4				1	
Bird	Raptor															
	Spilornis cheela					1								1		
	Accipiter trivirgatus													4		
	Corvid bird															
	Dendrocitta formosae									2			1			
	Cuckoo															
	*Cuculus optatus**													1		
Macaque	*Macaca cyclopsis*					1		1		1	1			2		
Other Mammal	Carnivore															
	Paguma larvata taivana					2								1		
	Herpestes urva			1		1		1						1		
	Rodent															
	Callosciurus erythraeus		1													
	Niviventer coningi													1		
Ant	-							1								
Total		1	6	4	1	9	2	5	2	3	11	1	3	20	1	1

*According to Ding *et al.* (2013), we treated the *Cuculus saturatus* described in Chen *et al.* (2009) as *Cuculus optatus*.

Snakes were the major predators for both shrub (61.9%) and ground (64.3%) nests (Table 2, Fig. 3). Avian predators (21.4%, *Z*=2.94) focused on shrub nests while mammalian predators (21.4%, *Z*=0.71) preferred ground nests. Macaques preyed on ground (7.1%) and shrub nests (9.5%, Fig. 3) equally. Snakes and macaques did not have preference between eggs or young while the raptors and other mammals focused on the young in the nests (Table 2).

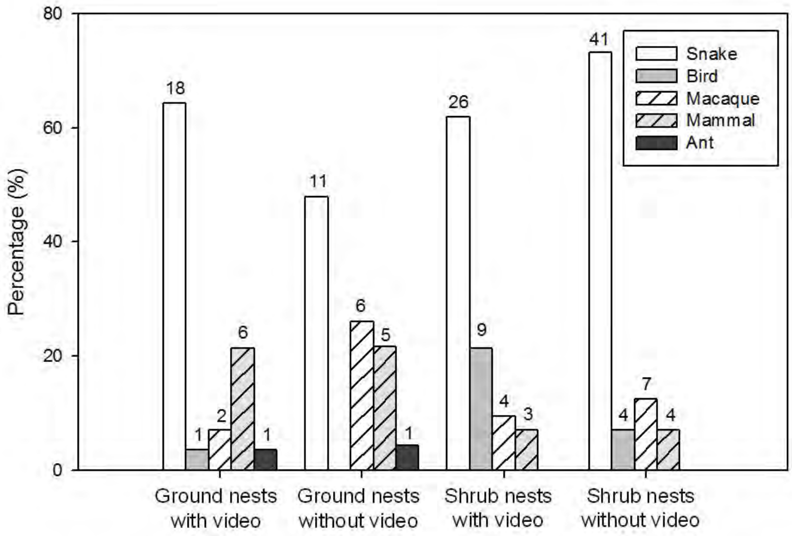


Fig. 3. Percentage of ground and shrub nests prey by the five predator groups. The actual number of nests in each category is shown at the top of the bars.

In the shrub nests, the daily predation rate (0.052±0.008, 38 depredated nests, 767 observed days) at 58 nests with video observation was similar to that at 85 regularly visited nests without video observation (0.070±0.009, 55 depredated nests, 858 observed days; $\chi^2 = 2.273$, $p = 0.132$). In contrast, the daily predation rate (0.023±0.005, 26 depredated nests, 1091 observed days) at 61 ground nests with video observation was significantly lower than that at 30 ground nests without video observation (0.079±0.017, 19 depredated nests, 252.5 observed days; $\chi^2 = 8.523$, $p = 0.004$).

The predator identification guidelines

We generalized the predator identification guidelines using video photography and field experience (Fig. 4). First, we observed the surrounding area of the nest preyed to determine if it was clean or messy. If the environment was disturbed or there were some animal footprints and tracks, we would categorize them as a mammalian predator. Mammal footprints and the remnants they left in the nests also helped to know what had happened. The location and breeding stage of nests would also help to classify the predators. Carnivores hunted nestlings in ground nests (57%), but raptors preferred nestlings in shrub nests (83%, Table 2). Then, we recorded the nest remnants to classify the potential predator type.

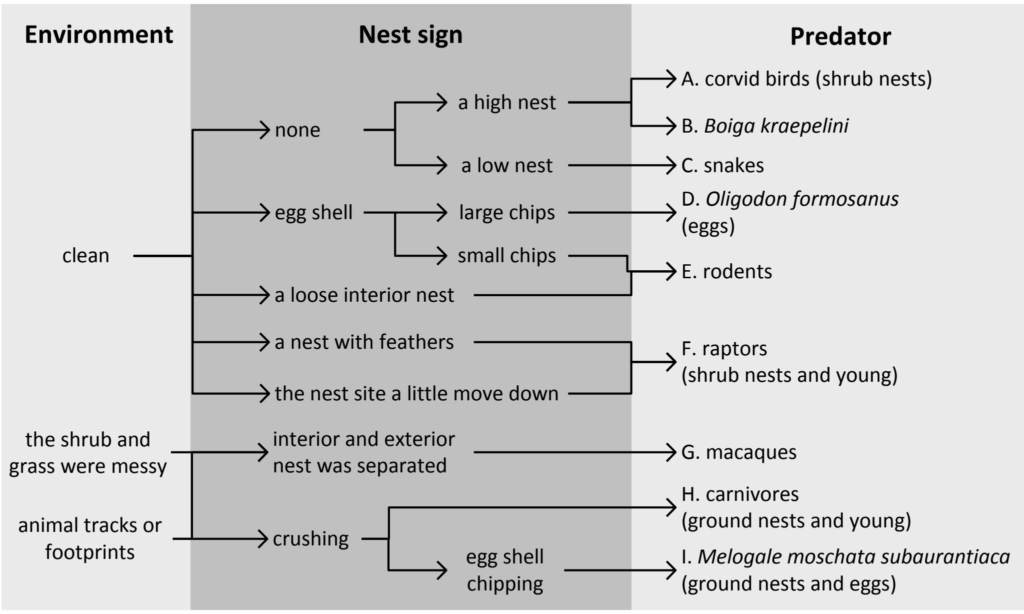


Fig. 4. Guidelines to identify the shrub and ground nest predators by the signs left in the environment and in and around the nest. The characteristics in parentheses were the preferences of predators for the prey. The video and nest photographs were given in Appendix A.

Snakes were both the major predators of the shrub and ground nests. *Boiga kraepelini*, a typical tree snake capable of climbing trees, was the most frequent predator (n=18). *O. formosanus* would leave a special remnant after eating eggs which consisted of tooth marks made by its specialization maxillary teeth left on the eggshell as if it had used a can-opener. Other snakes would usually swallow all the eggs or chicks in the nest, and did not leave any signs around the nest and also kept the empty nest unperturbed. Sometimes, the chicks were too large to swallow so that the suffocated bodies would be left near nests. Although most remnants left by snakes were not obvious, we would classify snake predation events by a clean and complete nest in the same surroundings as before.

Avian predators usually preyed on shrub nests and did not leave obvious evidence. After predation, the site of the shrub nest would be slightly moved downward. Three avian predator types were raptors, Corvidae and cuckoos. Raptors focused on the young and parents in the nests but ignored eggs. Feathers of the abdominal stuck on the rim of the nest after the raptor caught the parent bird incubating in the nest. Eggs and young both were preyed on by

Corvidae. A cuckoo (*Cuculus optatus*) was found to kill two nestlings but not eat them in a nest (Chen *et al*. 2009). The nestlings' bodies were left under the shrub nest. The only case of an avian predator preying on a ground nest was *Spilornis cheela* preying on a Fairy Pitta nest with five nestlings.

Macaca cyclopis is the only endemic species of macaques in Taiwan. In this study, they preyed on both shrub and ground nests in incubating and nestling stages. Macaques pulled down nests with their hands and casually threw them away onto the ground. The two layers (interior and exterior) of shrub nests would be separated by the macaques with hands. It was also easy to realize that macaques had visited the nest, because they would make messy shrubs and grasses after passing the surrounding area and usually pulled down the nests with their hands and casually threw nests away onto the ground near the original nest site.

Other mammalian predators included carnivores and rodents. Most carnivores preferred ground nests and nestlings. Carnivores would leave animal tracks and footprints that helped the identification. For example, *Melogale moschata subaurantiaca* searched prey with its nose and made a clear footpath by digging the soil. It would leave fragmented eggshells as a dominative sign after predation, and also pressed the nests or dug a hole on the bottom of ground nests. Rodents in Taiwan are much smaller than carnivores, so they would loosen the interior nest and leave chippings of egg shells.

We also recorded that ants preyed on a Dusky Fulvetta nest. However, we could not identify the species as the ants only appeared as tiny black dots on the monitor. The nest predation by ants might continue for several days, and could be observed directly that we had met the event once.

Considering the prey preference of each predator as well as the signs and remnants around the nests, we identified the shrub and ground nest predators in nests that were not monitored by video. Ninety-four shrub and 47 ground nests were classified into five predator types that included snakes, birds, macaques, other mammals and ants. The composition of predator groups was not different between the nests with and without video observation (χ^2 = 4.33, p = 0.363). Snakes were still the major predators, macaques equally preyed on shrub and ground nests, and birds and other mammals had similar preferences in their prey. Birds preferred shrub nests while other mammals attacked to ground nests (Fig. 3).

Discussion

In this study, we summarized environmental signs and nest remnants to construct a guideline that can help in identifying predator type in nest predation. These evidences can be applied to determine nest predators in similar environments and regions.

We found predation the major cause of nest failure in a Taiwan's lowland forest, although typhoons and rain storms also destroyed nests (3.7%). Occasionally, farmers (1.2%) carelessly broke the nests when managing their bamboo farmlands. Overall, predators hazarded the survival of passerines' nests in the forest. In Taiwan, snakes are the dominant nest predators, followed by other mammals, macaques and raptors. Our results are similar as those researches that snakes were more frequent nest predators at low latitudes (Pierce and Pobprasert 2013; DeGregorio *et al.* 2014). Our results are different from the temperate region where mammals, snakes, corvid birds are major predators, and nest parasitism by cowbirds and cuckoos are also common (Renfrew and Ribic 2003; Pietz and Granfors 2005; Benson 2010). Since regional predators depend on the local fauna, a complete list of local fauna is the first step to estimate the predation risk of nests. Using infrared cameras, we determined the nest predators that included Formosan macaques (*Macaca cyclopis*), Formosan ferret-badgers (*Melogale moschata subaurantiaca*), Formosan gem-faced civets (*Paguma larvata taivana*), Formosan crab-eating mongooses (*Herpestes urva*), Formosan wild boars (*Sus scrofa taivanus*), and rodents. These species are common in the Hushan reservoir near our study area (Cheng 2008).

The fact that the daily predation rate of shrub nests was higher than that of ground nests may be a reflection in such open habitat with scattered trees, dense shrubs and open canopy. In this habitat type, predators can easily detect the nests from above.

We found that the daily predation rate in ground nests was significantly different between those observed by the video system and the human while those in shrub nests showed no difference, that was similar to the results of Williams and Wood (2002), and Stake and Cimprich (2003). Using the video system underestimated the daily predation rate in ground nests and it suggests that using the video system alone may not be sufficient to understand the daily predation pattern and it is necessary to conduct direct field observation.

We monitored the real nests in the field that could reflect a real nest predation situation. Although the daily predation estimates maybe similar between artificial and real nests, predators differed substantially in their predation of artificial versus real nests. In addition, artificial nests also presented the biological bias in the predator assemblage that could not detect the existence of snakes (Thompson III and Burhans 2004). Several studies on artificial nests' studies did not detect snakes in the tropical and subtropical region (Wong *et al.* 1998; Hausmann *et al.* 2005; Pangau-Adam *et al.* 2006). Snakes were the most important predators of many real nests of tropical forests (Stake and Cimprich 2003; Stake *et al.* 2004; Staller *et al.* 2005). Ignoring snakes might cause serious bias when estimating nest predation risks.

Nest preferences in predator faunas

Although snakes were the major predators in both shrub and ground nests, we found differences between shrub and ground nests in the predator assemblage. Avian predators focused on shrub nests and rarely plundered eggs and young in the ground nests (Söderström *et al.* 1998; Hausmann *et al.* 2005). We only recorded raptors preying on nestlings and parent birds, and left eggs in the nests, but Gray Treepies (*Dendrocitta formosae*) which belongs to Corvidae would also prey on eggs and chicks. These visual hunters took mainly the conspicuous shrub nests (Weidinger 2002) and ignored the more cryptic ground nests. Other mammals preyed on the young in ground nests and shrub nests that were close to the ground.

Each type of predator searches for prey in a different manner. Avian predators locate nests using visual cues, and macaques also search for prey by visual cues. Other mammals apply olfactorial cues when locating prey (Hausmann *et al.* 2005). Thermoreceptors are present in snakes, which help to detect their prey (De Cock Buning 1983; Campbell *et al.* 2002). Thermoreceptors may be the reason of the detecting bias in artificial nests, because snakes could not detect those nests without living beings inside.

Applying the video system to detect predation pattern did not increase the daily predation rate (Brown *et al.* 1998; Thompson III *et al.* 1999) and also did not affect the composition of the predator faunas. Similar to Stake and Cimprich (2003), we also found no evidence that the video system would be used by predators as a cue to search the nests, and predators did not notice the video camera while they preyed on nests. The lower predation risk of video-taped nests could be explained that we only used video for the active nests and avoided those nests which failed in the early stages (i.e., laying and incubation) (Stake and Cimprich 2003).

The video system monitored the predatory situation of nests effectively. Using the video photography, we identified 17 species of nest predators, yielding a unique predator assemblage and showing the high nest predation risk in Taiwan. One limitation of this type of predator identification was the growth of plants that blocked the nest. In these cases we only obtained shadows and obscure photographs while predators were visiting nests. We could only identify to the predator types by the patterns and shapes, but not to species.

Signs left at nests by predators

After a nest predation event, predators would leave their characteristic traces around the nest, and rarely did the bird parents come back to the nest and move these remnants. The evident signs could be kept in the nests and used to determine the nest’s fate. The evident sign we used to identify the snake species is serrated eggshells left by *O. formosanus*. Otherwise most other snakes left no evidence as they usually left only an empty nest that could be classified as snake predation events. The adult’s feathers left on the rim of the nest were also a clear sign that a raptor caught a parent bird from a breeding nest. Macaques would leave a mess around the nests and usually pulled down nests by their hands and casually threw nests away on the ground near the original nest site. Mammalian footprints and the remnants they left in the nests also helped us to surmise what happened.

The actions of ants were rare events especially it is hard to identify them. Ants moved eggs or nestlings piece by piece and left nests clean with no remnants after their predation. To identify the ant species was impossible unless we visited the nests. *Crematogaster* sp. was found to prey on broken eggs of Grey-cheeked Fulvetta (W. J. Chen 2007, *personal observation*). In the videos, we saw many small black spots covering the nest and realized that they were ants, but we could not identify the species. Similar to snakes, ants also left nothing but an empty nest, but the predatory action would continue several days.

The video photography recorded clear evidence of nest predators and obtained stronger data than field identification. However, some minimum fieldwork is still necessary. The monitor can be used to check the stage of nests and reduced the frequency to revisit the active nest. The system causes hardly any nest failure with minimal disruption to nest site or adults (Thompson III *et al.* 1999; Renfrew and Ribic 2003; Stake and Cimprich 2003; Sabine *et al.* 2005). The disadvantage of applying the video-monitoring is its cost.

Based on fieldwork, we could identify the type of predator based on the remnants of the nests after the predation events. However, to make a sound link between the nest remnants and the predator, we needed the video system to fully understand the relationship between predators and prey. Thus, just using the signs to determine predator type was not reliable.

Acknowledgments

This study was partially supported by Endemic Species Research Institute, Council of Agriculture, National Science Council (now Ministry of Science and Technology), and the Central Water Resources Office, Water Resources Agency, Ministry of Economic Affairs, Taiwan. We also thank Jin-Kai Chang, Rui-Yuan Gu, Xu-Liang Zeng, Wen-Jay Chih, Hsin-Yi Chang and Cha-Hung Chen for their assistance with fieldwork.

Literature Cited

Aebischer, N. J. 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. Bird Study 46:22-31.

Auer, S. K., R. D. Bassar, J. J. Fontaine, and T. E. Martin. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. Condor 109:321-333.

Benson, T. J. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79:225-234.

Brawn, J. D., G. Angehr, N. Davros, W. D. Robinson, J. N. Styrsky, and C. E. Tarwater. 2011. Sources of variation in the nesting success of understory tropical birds. Journal of Avian Biology 42:61-68.

Brown, K. P., H. Moller, J. Innes, and P. Jansen. 1998. Identifying predators at nests of small birds in a New Zealand forest. Ibis 140:274-279.

Campbell, A. L., R. R. Naik, L. Sowards, and M. O. Stone. 2002. Biological infrared imaging and sensing. Micron 33:211-225.

Chen, W.-J., P.-F. Lee, and R.-S. Lin. 2009. The first record of a Himalayan cuckoo (*Cuculus saturatus*) killing nestlings in a potential host's nest. Endemic Species Research 11:63-67.

Cheng, H.-C. 2008. A list of mammals, their distribution and current status in the Hushan Reservoir area. Central Water Resources Office, Water Resources Agency, Ministry of Economic Affairs, Taiwan.

Cooper, D. S., and C. M. Francis. 1998. Nest predation in a Malaysian lowland rain forest. Biological Conservation 85:199-202.

Cutler, T. L., and E. S. Don. 1999. Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27:571-581.

De Cock Buning, T. 1983. Thermal sensitivity as a specialization for prey capture and feeding in snakes. American Zoologist 23: 363-375.

DeGregorio, B. A., S. J. Chiavacci, P. J. Weatherhead, J. D. Willson, T. J. Benson, and J. H. Sperry. 2014. Snake predation on North American bird nests: culprits, patterns and future directions. Journal of Avian Biology 45:325-333.

Ding, T.-S., C.-S. Juan, R.-S. Lin, C.-Y. Pan, Y.-J. Tsai, J. Wu and Y.-H. Yang. 2013. The 2013 CWBF checklist of the birds of Taiwan. Chinese Wild Bird Federation. Taipei, Taiwan.

Gibbs, J. P. 1991. Avian nest predation in tropical wet forest: an experimental study. Oikos 60:151-161.

Hanski, I. K., T. J. Fenske, and G. J. Niemi. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. Auk 113:578-585.

Hausmann, F., C. P. Catterall, and S. D. Piper. 2005. Effects of edge habitat and nest characteristics on depredation of artificial nests in fragmented Australian tropical rainforest. Biodiversity and Conservation 14:2331-2345.

Hazler, K. R. 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. Auk 121:707-716.

Hazler, K. R. 2006. Factors influencing Acadian flycatcher nesting success in an intensively managed forest landscape. Journal of Wildlife Management 70:532.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield Method of Estimating Nesting Success: A Model, Estimators and Simulation Results. Wilson Bulletin 93:42-53.

Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery rate estimates. US Fish & Wildlife Service, Fish & Wildlife Technical Report 24, Washington, D.C., USA.

Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897-913.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27:263-272.

Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.

Martin, T. E., C. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. Bbird field protocol - Breeding biology research and monitoring database. Montana Cooperative Wildlife Research Unit.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 78:255-261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Melville, H. I. A. S., W. C. Conway, M. L. Morrison, C. E. Comer, and J. B. Hardin. 2014. Artificial nests identify possible nest predators of eastern wild turkeys. Southeastern Naturalist 13:80-91.

Pangau-Adam, M. Z., M. Waltert, and M. Mühlenberg. 2006. Nest predation risk on ground and shrub nests in forest margin areas of Sulawesi, Indonesia. Biodiversity and Conservation 15:4143-4158.

Part, T., and J. Wretenberg. 2002. Do artificial nests reveal relative nest predation risk for real nests? Journal of Avian Biology 33:39-46.

Peterson, B. L., B. E. Kus, and D. H. Deutschman. 2004. Determining nest predators of the Least Bell's Vireo through point counts, tracking stations, and video photography. Journal of Field Ornithology 75:89-95.

Pierce, A. J., and K. Pobprasert. 2013. Nest predators of Southeast Asian evergreen forest birds identified through continuous video recording. Ibis 155:419-423.

Pietz, P. J., and D. A. Granfors. 2005. Parental nest defense on videotape: more reality than "Myth". Auk 122:701-705.

Rader, M. J., T. W. Teinert, L. A. Brennan, F. Hernández, N. J. Silvy, and X. B. Wu. 2007. Identifying predators and nest fates of bobwhites in southern Texas. Journal of Wildlife Management 71:1626-1630.

Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. Auk 120:371-383.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

Söderström, B., T. Pärt, and J. Rydén. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. Oecologia 117:108-118.

Sabine, J. B., J. M. Meyers, and S. H. Schweitzer. 2005. A simple, inexpensive video camera setup for the study of avian activity. Journal of Field Ornithology 76:293-297.

Sodhi, N. S., K. S. H. Peh, T. Ming Lee, I. M. Turner, H. T. W. Tan, D. M. Prawiradilaga, Darjono, and Darjono. 2003. Artificial nest and seed predation experiments on tropical Southeast Asian islands. Biodiversity and Conservation 12:2415-2433.

Stake, M. M., and D. A. Cimprich. 2003. Using video to monitor predation at black-capped video nests. Condor 105:348-357.

Stake, M. M., J. Faaborg, and F. R. Thompson III. 2004. Video identification of predators at Golden-cheeked Warbler nests. Journal of Field Ornithology 75:337-344.

Staller, E. L., W. E. Palmer, J. P. Carroll, R. P. Thornton, and D. C. Sisson. 2005. Identifying predators at northern bobwhite nests. Journal of Wildlife Management 69:124-132.

Thompson III, F. R., and D. E. Burhans. 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. Conservation Biology 18:373-380.

Thompson III, F. R., W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. Auk 116:259-264.

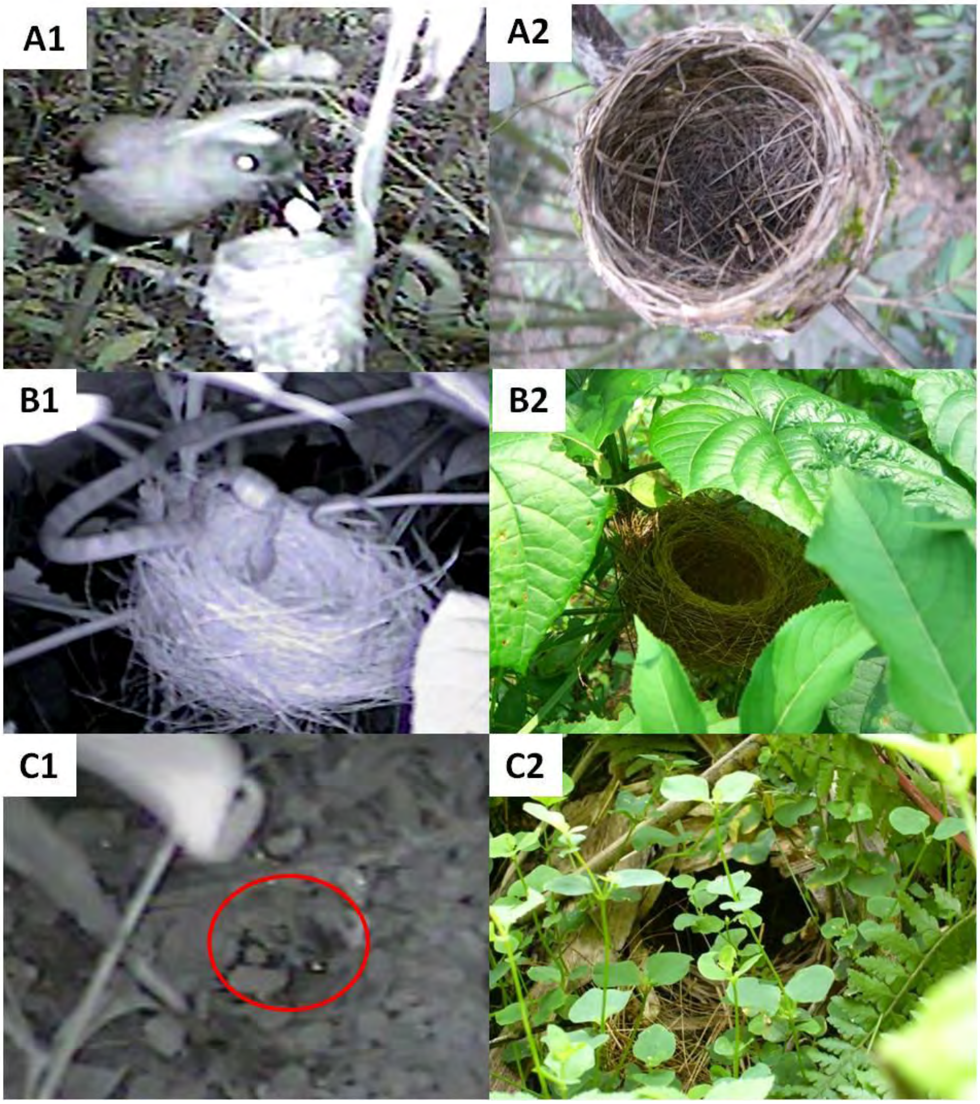
Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424-437.

Wikelski, M., M. Hau, W. D. Robinson, and J. C. Wingfield. 2003. Reproductive seasonality of seven neotropical passerine species. Condor 105:683-695.

Williams, G. E., and P. B. Wood. 2002. Are traditional method of determining nest predators and nest fates reliable? An experiment with wood thrushes (*Hylocichla mustelina*) using miniature video cameras. Auk 119:1126-1132.

Wong, T. C. M., N. S. Sodhi, and I. M. Turner. 1998. Artificial nest and seed predation experiments in tropical lowland rainforest remnants of Singapore. Biological Conservation 85:97-104

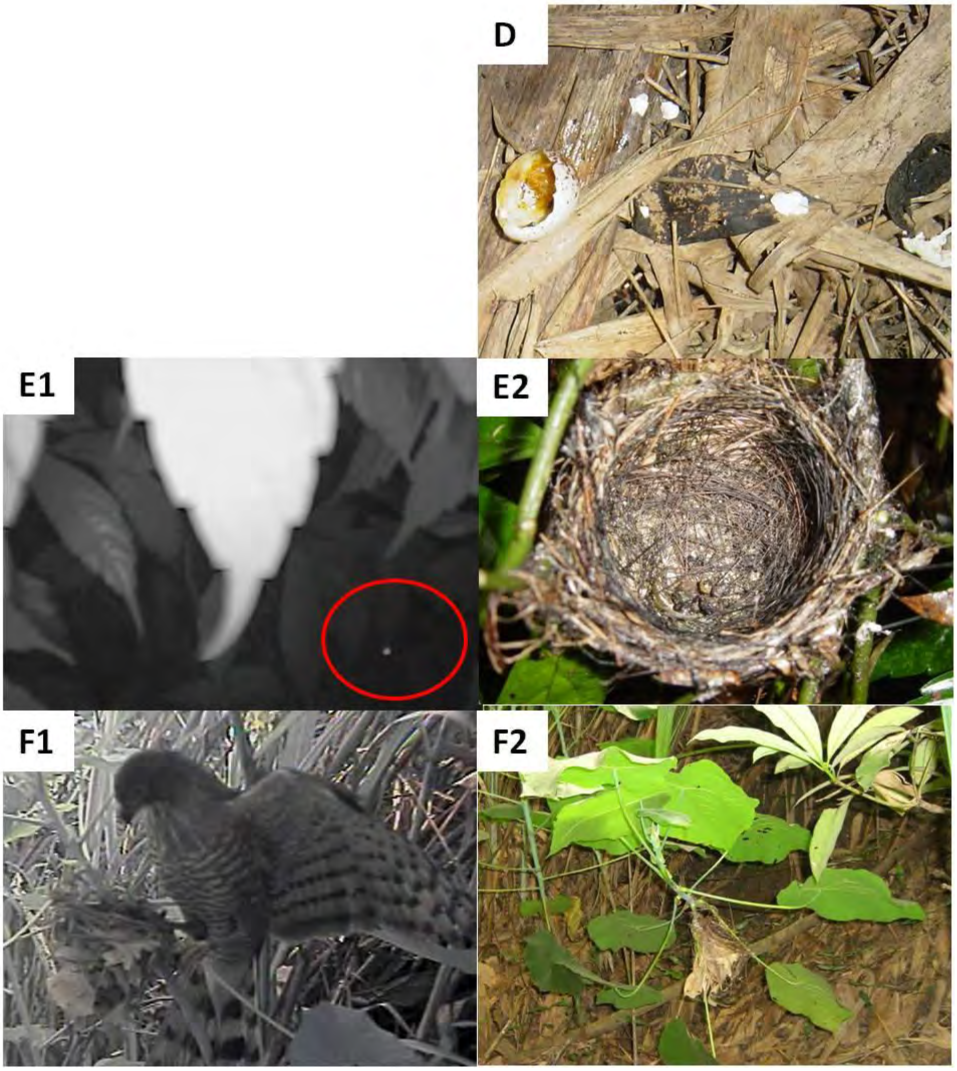
Appendix A. The video photography and nest photographs showing various predation type present:



A1. *Dendrocitta formosae* swallowed eggs of Black-naped Monarch (*Hypothymis azurea*) and left a clean nest (**A2**).

B1. *Boiga kraepelini* swallowed eggs of Light-vented Bulbul (*Pycnonotus sinensis*) and left a clean nest (B2).

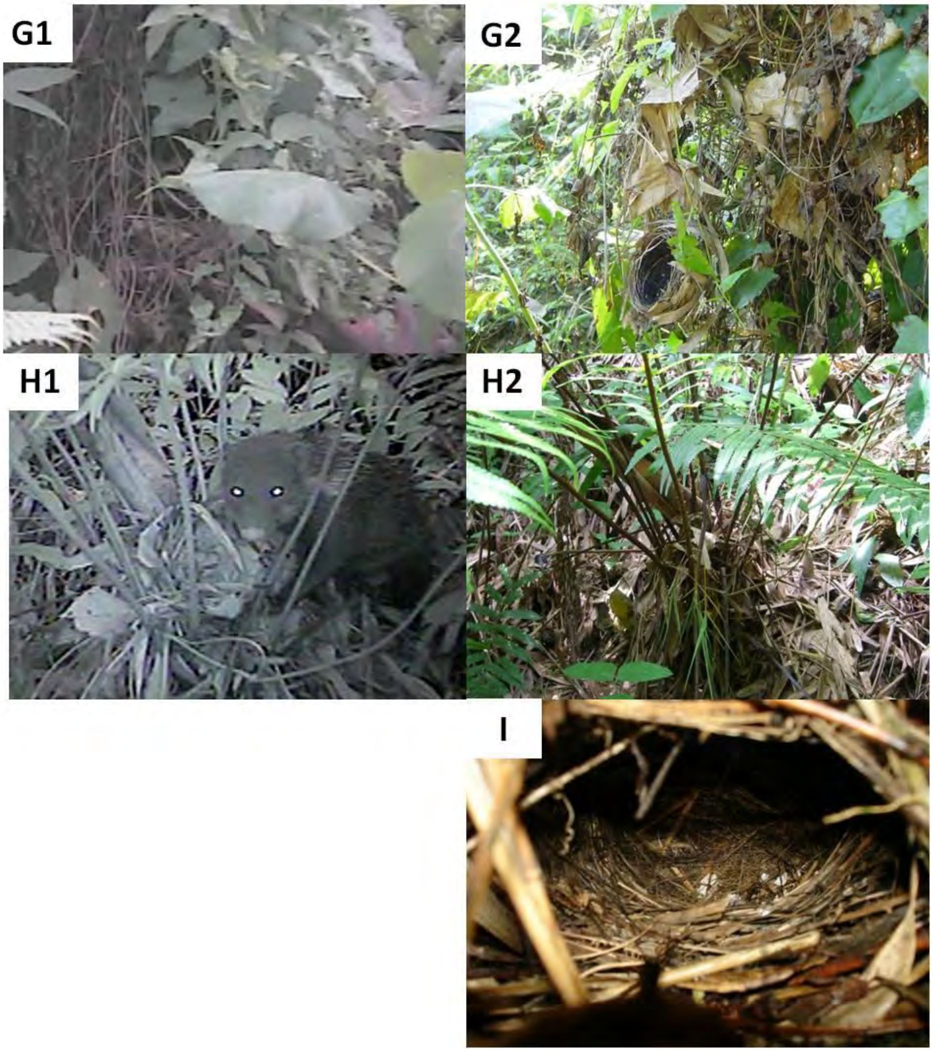
C1. *Protobothrops mucrosquamatus* preyed on the young of Taiwan Scimitar-Babbler (*Pomatorhinus musicus*) and left a clean nest (**C2**).



D. *Oligodon formosanus* preyed on eggs of Fairy Pitta (*Pitta nympha*) and left serrated eggshells around nests.

E1. A rodent preyed on the young of Grey-cheeked Fulvetta (*Alcippe morrisonia*) and left a loose interior nest (E2).

F1. *Accipiter trivirgatus* preyed on the young of Grey-cheeked Fulvetta (*Alcippe morrisonia*) and shifted the nest location a little downward (**F2**).



G1. *Macaca cyclopsis* preyed on the young of Grey-cheeked Fulvetta (*Alcippe morrisonia*) and messed up the shrub and the nest site (**G2**).

H1. *Herpestes urva* preyed on the young of Dusky Fulvetta (*Schoeniparus brunneus*) and crushed the nest (**H2**).

I. *Melogale moschata subaurantiaca* preyed on the eggs of Taiwan Scimitar-Babbler (*Pomatorhinus musicus*) and left chipped egg shell.