Reproductive ecology and nest-site selection of Siamese fireback in lowland forest

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Abstract. Breeding success in birds is strongly affected by the selection of suitable nesting sites which has the ability to directly affect population dynamics within a given population. Nest-sites are generally selected to reduce the risk of nest predation. In this study we provide information on the reproductive biology of Siamese fireback (*Lophura diardi*) at Sakaerat Biosphere Reserve, Thailand and identify habitat characteristics that influence nest site selection. At this site the species is found both in pristine and disturbed habitats. During a three year period (2010–2012), we found 21 nest-sites. Egg laying occurred from April to early August and the average clutch size was 6.4 ± 0.3 SE eggs (range four-eight). Incubation lasted 23–24 days and daily nest survival was estimated at 0.90 ± 0.02 SE (95% CI = 0.85–0.94), giving an estimated overall nest success of 0.08 ± 0.04 SE. Predation was the main cause of nest failure. Siamese fireback appeared to prefer to site nests between the buttresses of large trees (62.5%), which presumably have the potential to serve as shelter from potential predators. Analyses indicated that Siamese fireback significantly preferred to place nests in an area associated with dense vegetation coverage below 0.5 m, on steeper slopes, large basal areas of trees DBH >10 cm and with low potential predation pressure. This can be interpreted as a strategy to make the nest less conspicuous to predators and facilitate flying out of the nest when predators attack. Primary forest provides large mature trees and a complex structure of understory coverage that is important for optimal nesting sites and nest survival of Siamese fireback.

Key words. breeding ecology, daily nest survival, *Lophura diardi*, nesting success, Sakaerat Biosphere Reserve, the nest concealment hypotheses

INTRODUCTION

Nest-site selection is an important factor for species survival and reproductive success in birds (Clark & Nudds, 1991; Badyacv, 1995). Although there are many factors affecting nesting success (such as the health of the female, food availability, inflection, weather, etc.), predation appears to be the main cause of nest failure in several bird species (Descamps et al., 2005; Donehower et al., 2007; Pierce & Pobprasert, 2013). Birds choose nest sites non-randomly with respect to vegetation characteristics (Martin & Roper, 1988; Holway, 1991; Knopf & Sedgwick, 1992), and some may preferentially select nest sites with lower predation risk (Martin, 1992; Siepielski et al., 2001). Thus, vegetation structure is usually considered to be important for nest site selection of many birds (Bentzen et al., 2009; Kolada et al., 2009; Pobprasert & Gale, 2010; Wang et al., 2011; Yi-qun & Nai-fa, 2011) since, according to the nest concealment hypothesis, predation risk decreases in relation to high vegetation density around the nest site as vegetation density has been suggested to conceal the nest and interfere with visual, auditory, or chemical detection by predators (Martin, 1993).

However, beside vegetation density, ground structure affects nest site selection as it might play a role in predator avoidance. Ground-nesting birds often place their nests beside objects or clumps of vegetation (Lloyd et al., 2000). Suggested advantages of this pattern are protection from both nest predators and environmental conditions (Hockey, 1982; With & Webb, 1993). Many species, particularly within the order Galliformes, are precocial ground-nesting species which are particularly vulnerable to predation during nesting and brood-rearing (Hill & Robertson, 1988; Riley & Schulz, 2001; Draycott et al., 2008). Several studies have shown that predation is the principal cause of nesting mortality in Galliformes (Tapper et al., 1996; Jimenez & Conover, 2001; Draycott et al., 2008; Pierce & Pobprasert, 2013).

Siamese fireback, *Lophura diardi*, is a lowland species that nests on the ground (Johnsgard, 1999). This species was listed as Least Concern (IUCN, 2012). Although the population is considered to be undergoing a slow to moderate decline as a result of lowland habitat alteration and degradation including hunting (BirdLife International, 2012), the number of Siamese firebacks recorded at higher elevations (>800 m) in Khao Yai National Park, Thailand have increased significantly over the past 20 years (Round & Gale, 2008). The species has been reported to be polygynous in the wild (Savini & Sukumal, 2009) with the presence of solitary male

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floaters and multi-male groups (Suwanrat et al., in revision). A recent study of a sub-montane population of Siamese fireback revealed that the preferred nesting situation was on the ground in the buttresses of large trees and on steeper slopes (>10 degrees) areas and the study group showed a 45% nest success (Sukumal et al., 2010).

Although there have been few studies on ranging behavior and breeding ecology of Siamese firebacks, their nest-site selection remains unclear because of a small sample size and the limited number of studies undertaken in their natural range (Sukumal et al., 2010). Moreover, no quantitative data regarding different aspects of the breeding ecology of any *Lophura* species in tropical region exists. Therefore, identifying micro-habitat variables associated with nest-site selection and nest survival is important to understand bird-habitat relationships not only for Siamese fireback but also for other *Lophura* species.

In this paper we first provide basic information on the breeding ecology of this poorly known species including nesting period, clutch size, incubation period and nest success in their main lowland forest habitat. Second, we examine the relationship between micro-habitat characteristics and nest site selection, focusing on determining which ecological features of the habitat influence nest-site selection. Finally, we describe how predation pressure may relate to nest-site selection. Based on a previous study (Sukumal et al., 2010), we predict that in order to limit predation pressure, nest sites will be located in positions associated with: 1) a higher degree of slope to facilitate flying out of the nest when predators attack; and 2) a higher nest concealment to make the nest less conspicuous to predators.

METHODS

Study site. The study was conducted at Sakaerat Environmental Research Station (SERS), classified as a UNESCO Biosphere Reserve since 1967. The reserve, covering 78.09 km², is located in north-eastern Thailand (14°30'N and 101°55'E) on the edge of Thailand's Khorat Plateau at an elevation of 280–762 m above sea level. SERS has two major natural forest types: dry evergreen forest (60%) dominated by tree species such as *Hopea ferrea*, *Hopea odorata*, and *Hydnocarpus ilicifolia*, and dry dipterocarp forest (18%) dominated by common dipterocarp trees such as *Shorea siamensis*, *Shorea obtusa*, and *Dipterocarpus intricatus*, as well as two large patches of more than 20 year old forest plantation of mixed acacia and eucalyptus (18%), and several small patches of bamboo forest (1%), grassland (1%), and the office and operational buildings (2%) (Thailand Institute of Science and Technology, 2012). The study area is of approximately 3 km² dominated by dry evergreen forest, located beside the 3–6 km mark of the main road, with elevation ranging between 350–580 m. Average annual precipitation is 1200 mm with a dry season from November to April (average rain fall 210 mm) and a wet season from May to October (average rainfall 860 mm), with rainfall peaks in May and September. Average annual temperature is 26.1°C (range 19.3 to 32.8°C) and average

relative humidity is 82.2% (range 74 to 87%) (Suwanrat et al., in revision).

Nest finding. During three breeding seasons (2010–2012), we searched for the nests of Siamese fireback within eight home ranges defined by following radio-tagged birds (for details see Suwanrat et al., in revision). To find nests we either followed radio-tagged females or searched at the base of tree buttresses where they are known to nest (Sukumal et al., 2010). A few nests were found opportunistically while doing other field work. Eight females, belonging to eight different groups, had previously been captured using mist nets or modified traditional leg snare traps made from bamboo and polyester string. One female was caught in 2010 and the others in 2011. All birds caught were banded with a unique combination of two or three colors and one metal ring (11A size, Department of National Park Wildlife and Plant Conservation), and fitted with a 15 g necklace-type radio-transmitter (model RI-2B, Holohil System Ltd.). Transmitter life was approximately 24 months. Nests were located by tracking the birds to their nests using ATS R410 receivers with a three-element hand-held Yagi antenna.

Nest monitoring. Once a nest was located, the position was recorded using a global positioning system (GPS). On subsequent visits, nests were checked from >20 m to avoid accidentally flushing the female. Each nest was checked every two to three days during the incubation stage to determine if it was still active or had failed. Successful nests were defined to have the presence of large eggshell fragments in a nest (Lu & Zheng, 2003), indicating at least one egg had hatched or by the presence of chick(s) with a female bird, while unsuccessful nests were indicated by a deserted clutch, missing clutch or small eggshells scattered around the nest during the incubation period. Bird remains or large feathers at the nest site were taken to indicate that the incubating bird had been killed or injured by predators. We defined the nesting period for the population as the time when the first nest was found until the last active nest failed or hatched, and the incubation period for the individual as the time when the female started incubating until the hatching of the first egg.

Habitat measurements. For each nest site, we recorded the following variables: type of background (i.e., in tree buttress, under bushes, under the rocky outcrops), nest tree species and their diameter at breast height (DBH). Habitat characteristics surrounding the nesting trees were measured within 5-m and 10-m radius circular plots centered on the nesting site following Martin et al. (1997) and Sukumal et al. (2010). Within a 5-m radius circular plot, we collected information on slope degree measured with a clinometer and counted the number of woody climbers and all understory stems (DBH ≤10 cm), which were categorised into four classes based on their height: 0.5–1, >1–3, >3–5, and >5 m. We also estimated the percentage of vegetation cover for each height category including the percentage of ground covered by vegetation that is below 0.5 m in height. Within a 10-m radius circular plot, we measured the DBH of trees with DBH >10 cm in order to estimate basal area. The habitat measurements at nest sites were taken after hatching or nest

failure. All vegetation cover estimates were measured by one observer (J. Suwanrat).

To estimate the availability of nesting habitats, 60 control plots were systematically chosen over known home ranges and we took the same measurements as those at nest-sites. The control plots were located 300 m apart (Fig. 1), which is considered to be the approximate width of a home range of Siamese fireback (Sukumal et al., 2010).

Predator abundance. We placed automatic camera traps throughout the study area in order to estimate distribution of Siamese fireback at a larger scale and to estimate the relative abundance of potential predators. We took the potential predators of Siamese fireback to be all small carnivores and other potential nest predators based on the list by Pierce & Pobprasert (2013). Camera trapping was conducted during two breeding seasons (February–May) in 2010 and 2011. We used passive infrared camera traps with flash (Stealth Cam, TX, USA), including the date and time stamp on each photograph. In 2010, we installed cameras at 46 locations in dry evergreen forest (DEF) and 10 locations in dry dipterocarp forest (DDF), while in 2011 we re-installed camera traps in 46 locations in DEF and installed 15 locations in forest plantation (FP). The systems were programmed to run for 24 h per day and to take nine consecutive pictures per detection. We set each camera trap at least 700 m apart, and these were left in place for 14 days (except for a month in DDF) and then retrieved. We defined independent events as consecutive photographs of individuals taken more than 30 minutes apart based on O' Brien et al. (2003). Previous studies using camera traps across a range of animal taxa have shown a strong correlation between abundance estimates and relative abundance estimates (O' Brien et al., 2003; Rowcliffe et al., 2008; Rovero & Marshall, 2009) but see Sollmann and co-authors (2013). In this paper, we interpreted the relative abundance index (RAI) as an index of frequency used area by potentials predators, meaning that the more predator
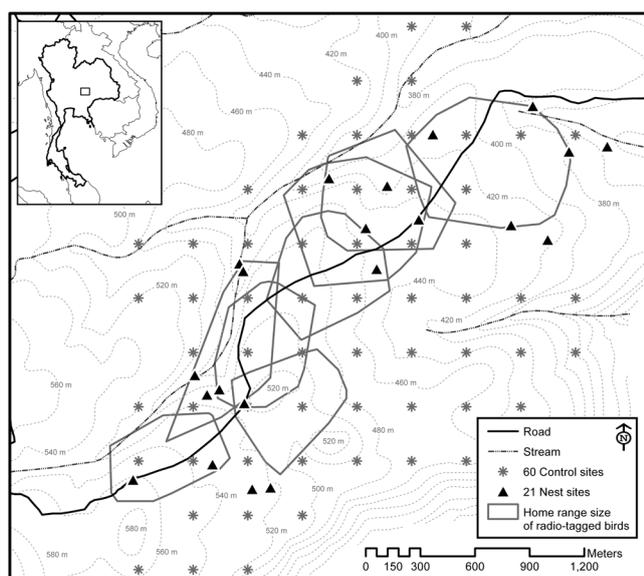

Fig. 1. Location of Sakaerat Environmental Research Station, Nakhon Ratchasima, Thailand including 21 nests and 60 control sites for nest-site selection of Siamese firebacks.

photos at any particular camera locations indicate a higher probability of predators detecting the nests in the same locations. We used the number of independent photographs of a species as an index of species frequency and calculated the RAI by dividing the number of independent photos with the total trap-nights for each camera trap location in different years. RAI was standardised to the number of photographs per 100 trap-nights.

We used the pooled photographs of all potential predator species divided by the total trap-nights for each camera trap location as a measure of predation pressure because of higher incidence of avian predators leading to low reproductive outcome (Eggers et al., 2006; Sparkman et al., 2013). We interpolated the surface of predation pressure across the whole study area by "Kriging" interpolation tool in the ArcGIS version 9.3 (ESRI, 2009) to generate predation pressure surface from camera trap locations for each year. Two interpolated surfaces were then averaged to create the final surface used to determine predation pressure surrounding the nest and control sites.

Data analysis. Average clutch size was calculated for each study year and for the study overall using information from all active nests. We only compared clutch-size between 2011 and 2012 because of the small sample size in 2010 ($N = 2$ clutches out of 3 nests found). Count data is a Poisson distribution by nature; for the comparison of clutch-size we used a non-parametric Mann–Whitney U-test. Nests found by following the eight radio-tagged females were used to calculate average clutch size per nest-attempted. From these estimates we excluded nests found by chance after the nests failed or hatched as their clutch size could not be determined. All the values given are mean ± standard errors (SE).

We modeled the daily survival rate (DSR) of Siamese fireback nests using the R Program 2.13.0 (R Development Core Team, 2011), with package RMark (Laake & Rexstad, 2008). Nests that were found after hatching or failure were excluded from this analysis ($N = 3$ nests), because we did not know exactly the fate of those nests. Due to our small sample of successful nests, we did not have sufficient statistical power to model the effect of nest survival from other covariates. We reported only the constant model assuming that all nests in the sample under consideration have the same daily survival rate for every day. Encounter histories were constructed following Rotella (2005), which required the following data for each nest: 1) the day the nest was found; 2) the last day the nest was checked when still active; 3) the last day the nest was checked; and 4) the fate of nest (success or failed). Days were standardised so that the earliest date across all years when a nest was first found was coded as day 1, with subsequent dates numbered sequentially relative to the first day (Rotella, 2005). To calculate overall nest success, we raised the estimated daily survival rate to a power equal to duration in days of incubation period. The standard error of nest success was calculated following Powell (2007).

We used a non-parametric Mann–Whitney U-test for comparisons of habitat variables and predation pressure

between the nests and control sites because our data are not normally distributed. The statistical tests are two-tailed and values given are mean ± SE. We used logistic regression to determine the variables influencing nest-site selection. Variables were transformed prior to analysis and vegetation cover was arcsine transformed (Sokal & Rohlf, 1995), while continuous variables were standardised by dividing the value by twice the standard deviation (Gelman, 2008). Variables were highly correlated ($r > 0.5$); we selected only one variable at a time to a fitted regression model. We developed a set of models to test our hypotheses that may explain the selection of nest sites based on hypotheses of nesting in the area with a higher degree of slope (Sukumal et al., 2010), higher nest concealment (Martin, 1993) and lower predation risk (Bekoff et al., 1989; Martin, 1998; Latif et al., 2012). All models were based on 12 habitat variables and predation pressure. We fitted the intercept model, a global model (including all variables) and the model specific assumption. Model selections were compared with the lowest second order of Akaike Information Criterion (AIC_c) value (Akaike, 1973). Akaike model weights (w_i), were calculated as the weight of evidence in favor of model i among the models being compared.

We evaluated the model classification accuracy using the area under the receiver operating characteristic curve, AUC (Hosmer & Lemeshow, 2000). We chose an optimal threshold cut-off value for classification based on the receiver operating characteristic curve using the minimised difference between the proportion of presences correctly predicted (sensitivity) and the proportion of absences correctly predicted (specificity) (Fielding & Bell, 1997). Model averaging was used to estimate the coefficients of uncertainty models ($\Delta AIC_c < 2$). We used 85% confidence intervals to identify variables with significant influence on nest site selection; this interval renders model selection and parameter-evaluation criteria more congruent than the narrower interval (95%) widths (Arnold, 2010). All statistical analyses were performed using the R Program 2.13.0 (R Development Core Team, 2011) with MASS package (Venables & Ripley, 2002), AICcmodavg package (Mazerolle, 2012) and PresenceAbsence package (Freeman & Moisen, 2008).

RESULTS

Nesting period, clutch size and incubation. We found a total of 21 nest-sites during three breeding seasons, three nests in 2010, 11 nests in 2011 and seven nests in 2012. Eighteen of these were active nests consisting of 16 nests found by following eight radio-tagged females and two nests found opportunistically, while the other three nests were found after they had failed or hatched judging from the presence of eggshell fragments. Considering the 18 active nests, the nesting period of Siamese fireback in 2010 could not be realistically determined as one nest was found on April 29 and the other was predated on May 5 ($N = 2$); in 2011 it started on April 1 and ended on August 1 ($N = 10$), and in 2012 it started on April 5 and ended on July 25 ($N = 6$). Thus, the results indicated that the laying period of

Siamese fireback in our study area occurred from April to early August.

The mean clutch size was 6.4 ± 0.3 eggs ($N = 18$ nests, pooled data from three breeding seasons) ranging from four to eight eggs. The clutch size was similar among years with an average of 6.5 ± 0.5 eggs ($N =$ two nests, maximum = seven eggs, minimum = six eggs), 6.6 ± 0.3 eggs ($N = 10$ nests, maximum = eight eggs, minimum = five eggs), and 6.0 ± 0.7 eggs ($N =$ six nests, maximum = eight eggs, minimum = four eggs) in 2010, 2011 and 2012 respectively. However, there was no significant difference in clutch size between 2011 and 2012 (Mann–Whitney U-test, W = 38.5, $P = 0.36$). In 2011, two radio-tagged females re-nested after their first nest failed. One relaying was successful while the other failed. In 2012, only one radio-tagged female re-nested, making a total of three attempts. Unfortunately, both nest and hen were predated during incubation in the last attempt. The average size of the first clutch (6.6 ± 0.3 eggs, $N = 12$ nests) was similar to the second clutch (6.0 ± 0.6 eggs, $N =$ three nests), while the clutch size of the third attempt was 4 eggs ($N =$ one nest). The average period between nest failure and re-nesting was 35.5 ± 3.8 days, ranging from 25 to 43 days. The incubation period, calculated from two successful nests, was 23–24 days.

Nesting success. Only 18 active nests were used to analyse nest success as their fate was accurately known. We obtained a daily nest survival rate of 0.90 ± 0.02 (95% CI = 0.85–0.94). Overall, nest success was 0.08 ± 0.04 with only two out of the 18 monitored nests hatched. Nest failure was due to predation on the clutch or on the hen. Although we do not know most of the nest predators in our study, we found evidence of failure at one nest as a result of reticulated python (*Malayopython reticulatus*). The python was found at the nest site with two intact eggs remaining. We believe that the adult female had already been predated while incubating judging from the python's distended body shape.

Predator abundance. Camera traps were active for a total of 1965 trap-nights (1157 trap-nights in 2010 and 808 trap-nights in 2011) and they photographed 116 independent detections (45 detections in 2010 and 71 detections in 2011) of 10 potential predators including Asian golden jackal *Canis aureus*, common palm civet *Paradoxurus hermaphroditus*, hog badger *Arctonyx collaris*, large Indian civet *Viverra zibetha*, large-spotted civet *V. megaspila*, small Indian civet *Viverricula indica*, leopard cat *Prionailurus bengalensis*, small Asian mongoose *Herpestes javanicus*, pig-tailed macaque *Macaca nemestrina* and Bengal monitor lizard *Varanus bengalensis* (Table 1). The most likely potential predators detected in 2010 were common palm civet, Asian golden jackal and pig-tailed macaque with RAI values of 1.73, 0.78 and 0.61 photos 100 trap-nights^{-1} respectively, whereas in 2011 were common palm civet, leopard cat and pig-tailed macaque with RAI values of 6.19, 0.87 and 0.87 photos 100 trap-nights^{-1} respectively. Although, the average RAI across the potential predators in 2010 (0.49 ± 0.20 photos 100 trap-nights^{-1}) was less than those in 2011 (1.26 ± 0.83

Table 1. Number of independent photos, the relative abundance index value (RAI, photos 100 trap-nights[-1]) and average RAI across species of potential predators of Siamese firebacks in SERS.

Potential Predators	2010 (1157 Trap-nights)		2011 (808 Trap-nights)	
	# Photos	RAI	# Photos	RAI
Asian golden jackal *Canis aureus*	9	0.78	–	–
Hog badger *Arctonyx collaris*	1	0.09	1	0.12
Common palm civet *Paradoxurus hermaphrodites*	20	1.73	50	6.19
Large Indian civet *Viverra zibetha*	–	–	3	0.37
Large-spotted civet *Viverra megaspila*	1	0.09	–	–
Small Indian civet *Viverricula indica*	2	0.17	–	–
Leopard cat *Prionailurus bengalensis*	4	0.35	7	0.87
Small Asian mongoose *Herpestes javanicus*	–	–	2	0.25
Pig-tailed macaque *Macaca nemestrina*	7	0.61	7	0.87
Monitor lizard *Varanus bengalensis*	1	0.09	1	0.12
Average across species	0.49 ± 0.20		1.26 ± 0.83	

Table 2. Comparison of habitat variables and predation pressure between Siamese Fireback's nest sites ($N = 21$ nest locations) and control sites ($N = 60$ control locations)

Habitat Variables	Nest Sites			Control Sites			Mann-Whitney *U*-test
	Mean	±	SE	Mean	±	SE	*P*-value
Slope (degree)	10.9	±	1.5	8.3	±	0.6	0.12
Tree coverage: height <0.5 m (%)	33.9	±	4.3	12.2	±	0.8	<0.001
Tree coverage: height 0.5–1 m (%)	25.8	±	3.5	12.3	±	0.7	<0.001
Tree coverage: height 1–3 m (%)	20.3	±	2.1	18.4	±	1.0	0.32
Tree coverage: height 3–5 m (%)	17.8	±	2.7	14.7	±	0.9	0.61
Tree coverage: height >5 m (%)	76.6	±	2.5	79.0	±	0.8	0.76
Tree density: height 0.5–1 m (stems)	63.1	±	7.9	79.9	±	0.8	0.05
Tree density: height 1–3 m (stems)	58.2	±	7.6	83.4	±	3.8	0.004
Tree density: height 3–5 m (stems)	12.5	±	1.6	13.8	±	0.8	0.34
Tree density: height >5 m (stems)	13.1	±	1.2	17.4	±	0.9	0.03
Number of woody climbers (stems)	12.6	±	2.2	12.3	±	0.9	0.94
Basal area[a] (m^2)	1.04	±	0.16	0.79	±	0.05	0.13
Predation pressure[b] (photos trap-night[-1])	0.11	±	0.01	0.16	±	0.01	<0.001

[a]Basal area of trees with DBH >10 cm recorded with in a 10-m radius circular plot.
[b]determining using camera trapping data

photos 100 trap-nights[-1]), there was no significant difference between years (Mann–Whitney *U*-test, W = 19, $P = 0.32$).

Nest-site selection. All nest-sites had a structure on one side of the nest, such as a tree trunk, rocky wall or dense bush. From the 16 nest-sites of the eight radio-tagged females, 10 nests (62.5%) were located between the buttresses of large trees, four nests (25%) were placed on the ground with dense bushes or grasses, one nest (6.25%) was located in a clump of rattan, and another nest (6.25%) was located between rocks. All three nests found by chance were between the buttresses of large trees as a result of particular effort in searching at such sites. The average diameter at breast height (DBH) of nest trees (in genera *Hopea*, *Irvingia*, *Parkia*, *Ficus*) was 185.4 ± 24.7 cm ($N = 15$ trees), ranging from 63.5 to 359.0 cm.

We compared the habitat variables between nest ($N = 21$ locations) and control sites ($N = 60$ locations; Table 2). Percentage cover of small trees (height <0.5 m and 0.5–1 m) at nest sites was significantly higher than at control sites, but densities of understory saplings (height 0.5–1 m and 1–3 m) and tall trees (height >5 m) were significantly less than those at control sites. In addition, predation pressure surrounding nest sites was significantly lower than surrounding control sites (Table 2).

A candidate set of 14 regression models were fitted to explain nest-site selection of Siamese fireback. The best model, based on ΔAIC$_c$ and AIC$_c$ wight (Table 3), included tree coverage at <0.5 m height, degree of slope, basal area of trees with DBH >10 cm and predation pressure which correctly predicted nest sites selection in 93.57% of these

Table 3. The confident set of multiple logistic regression models explaining nest-site selection of Siamese fireback. Cover0 is tree coverage at height <0.5 m, BA is basal area of trees with DBH >10 cm, Slo is degree of slope, and Prd is predation pressure.

Model	LL	K	$\triangle AIC_c$	w_i	AUC
(14 models tested)					
Cover0 + BA + Slo + Prd	−20.84	5	0.00	0.52	93.57
Cover0 + Slo + Prd	−22.65	4	1.35	0.27	92.14
Cover0 + BA + Slo	−23.41	4	2.87	0.12	90.16
Cover0 + BA + Prd	−24.36	4	4.77	0.05	89.60

LL is log-likelihood: K is number of parameters in the model: $\triangle AIC_c$ is difference in AIC_c (model score) value, model with $\triangle AIC_c$ value 0 has most support, value between 0 and 2 have substantial support, value greater than 2 have less support: w_i = Akaike model weights: AUC = area under the receiver operating characteristic curve.

Table 4. Estimates of coefficients derived from model averaging (averaged across all models that contain such variables) and unconditional SE and its 85% confidence interval.

Variables Estimated	Coefficient	Uncond. SE	Lower 85%	Upper 85%
Tree coverage at height <0.5 m	13.82[a]	3.91	8.20	19.44
Basal area of trees with DBH >10 cm	1.44	0.82	0.26	2.62
Degree of slope	2.24	0.95	0.86	3.61
Predation pressure	−2.61	1.23	−4.37	−0.84

Estimated coefficients of variables that suggest significant effects on nest-site selection of Siamese fireback. Overlap with zero indicates a weak effect or no effect.
[a]variable resulted from arcsine transformed while others resulted from standardised.

cases while the second best model including all these variables except basal area of large trees showed relatively high percentage of classification (AUC = 92.14%). Model averaging was estimated for the coefficients of those variables in the confidence set (Table 3) based on accumulated 95% model weight. Estimated coefficients for tree coverage at <0.5 m height, degree of slope and basal area of large trees was significantly positive, whereas the estimate for predation pressure was a significantly negative influence on nest site selection of Siamese firebacks (Table 4).

DISCUSSION

This study investigated the breeding biology of the Siamese firebacks in their main lowland forest habitat. Although much of what we found is similar to previous studies, our study provides the largest dataset of nest outcomes for *Lophura* sp. available in their natural forest habitat. In addition, we quantified nest survival rate of the Siamese firebacks, the first time this has been attempted for a *Lophura* sp., and found that nesting success during incubation period is particularly low, indicating high nest predation in our study area. Moreover, we attempted to determine nesting habitat for the lowland population in order to allow comparison with the population that has recently shown a range expansion into sub-montane forest habitat and prefers nesting on steep terrain (Sukumal et al., 2010). Although our study area was in relatively flat and less steep terrain, we found that not only steeper slope, but also higher percentage of tree coverage below 50 cm, higher basal area of large tree (DBH >10 cm) and low predation pressure were significant factors that influence nest-site selection of Siamese firebacks.

Nesting biology and success. In our study, the nesting period of Siamese firebacks occurred from April to early August. This period covered the nesting period for known lowland populations (Johnsgard, 1999; Madge & McGowan, 2002) and is longer than that reported for a sub-montane population (Sukumal et al., 2010). Siamese firebacks started to lay eggs approximately one month before the beginning of the wet season (in May). Their response could be interpreted as an adaptation to the variability in the onset of the wet season as rainfall can increase the numbers of some insects (Lowman, 1982; Nummellin, 1989; Leigh et al., 1996; Anu et al., 2009). So, nesting during wet season might provide sufficient food, both in abundance and quality, for the birds (Hau, 2001).

Our average clutch size of 6.4 ± 0.3 eggs was similar to previous reports (Madge & McGowan, 2002; Sukumal et al., 2010). Our small sample size and small variation in clutch size among years limited our explanations. In the scaly-breasted partridge (*Arborophila chloropus*) it has been observed that birds may respond to better conditions by laying eggs earlier and by laying a larger number of eggs per clutch (Ong-in, 2011). Information from Siamese fireback is consistent but not sufficient to confirm similar findings. Evolved clutch size is presumably largely a reflection of the average amounts of food available to the female around the time of nesting (Lack, 1968).

Reported incubation periods of Siamese fireback are 24 to 25 days in captivity (Madge & McGowan, 2002), and 23.5 days in the wild (Sukumal et al., 2010); our period from complete clutch to hatch was similar estimated at 23.5 days. However, the period in our study was based on a very small

sample (only two successful nests) from radio-tagged females. Incubation periods among pheasants range in length from 18 to 29 days, with the longer ones typical of such genera as *Argusianus*, *Pavo*, *Lophophorus*, and *Crossoptilon*, whereas periods of less than 23 days occur in forms such as *Pucrasia*, *Chrysolophus*, and *Polyplectron*, but in all cases only the female incubated (Delacour, 1977; Johnsgard, 1999).

The estimate of nest success was approximately 8%. Owing to the small sample of successful nests (N = two nests), we suggest that the estimate should be treated with caution. Nest success in our study was apparently lower compared with those of a sub-montane population (five of the 11 nests hatched, Sukumal et al., 2010). Nest success could vary with habitat type but a larger sample size would be needed for confirmation. Several studies have shown that predation is the main cause of nesting failure in Galliformes (Tapper et al., 1996; Jimenez & Conover, 2001; Draycott et al., 2008). For pheasants, the extended nesting period (egg laying and incubation) might pose a great risk to eggs and hens owing to a longer exposure to predators (Lu & Zheng, 2003; Draycott et al., 2008). Moreover, high predation rates could be the result of higher densities of potential predators (Reynold & Tapper, 1993) but we are not able to compare our results with an equivalent measure of predator pressure in the sub-montane population.

According to our camera trapping data, we found a diverse suite of potential predators. The most frequently detected predators were the common palm civets (60.3%) and pig-tailed macaques (12.1%). A previous study observed that pig-tailed macaque plays an important role as a nest predator in evergreen forest at Khao Yai National Park (Pierce & Pobprasert, 2013), in habitat similar to the forest complex of SERS. Owing to the relatively small size of the dry evergreen forest patch, in which our study site is included, we can predict that usually wide ranging predators, such as macaque and civets, might re-use the same part of their home range with higher intensity with the consequence of increasing their predator pressure on the nesting bird community. However, apart from mammal species, other animals species such as snakes, raptors and non-raptorial birds, squirrels, and tree shrews are potential predators of Siamese firebacks (Ong-in, 2011; Pierce & Pobprasert, 2013,). Practically, we could not detect those animals by camera-trapping. Although we did not have quantitative data regarding predators, we found evidence of the predation of a Siamese fireback during incubation by a reticulated python, which was similarly observed for female silver pheasant at Khao Yai National Park (Sukumal, 2009). Reports of predation by reptiles on pheasants are rare (Lind & Welsh 1990; Bezy & Enderson, 2003).

Nest-site selection. Our regression models indicate that Siamese firebacks prefers to nest in areas with dense vegetation coverage below 50 cm, on steeper slopes, with large basal area of tree DBH >10 m and low predation pressure (Table 3, 4). Preference for dense vegetation coverage at nest sites may be a response to predation risk, similar to other bird species that select nesting places in areas

with higher nest concealment in order to reduce predation risk (Martin, 1993). Vegetation concealment seems to represent important aspects of nest-site selection in ground-nesting birds, particularly pheasants such as white-eared pheasant (*Crossoptilon crossoptilon*) in southwestern Sichuan Province, China (Nan et al., 2006), blue-eared pheasant (*Crossoptilon auritum*) in southern Gansu Province, China (Yi-qun & Nai-fa, 2011), and Hume's pheasant (*Syrmaticus humiae*) in the Doi Chiang Dao Wildlife Sanctury, Northern Thailand (Iamsiri & Gale, 2008). This can be interpreted as a strategy to make the nest less conspicuous to predators by blocking the view of raptors and mammals at a distance.

Siamese firebacks showed high preference for steeper slopes for nest-site selection. Locating nests on steeper slopes can be interpreted as a strategy to make a nest less accessible to predators and facilitates flying out of the nest when predators attack (Lima, 1993; Sukumal & Savini, 2009). Selection of this pattern is commonly found among the Galliformes, including sub-montane Siamese fireback (Sukumal et al., 2010), silver pheasant (Sukumal & Savini, 2009), blue-eared pheasant (Yi-qun & Nai-fa, 2011), and white-eared pheasant (Wang et al., 2005). As suggested by Ong-in (2011), high preference of steeper slope for nest site selection of scaly-breasted partridge not only provides a good position from which to observe predators, but can also provide good drainage.

In addition, Siamese firebacks selected nest locations with tree DBH >10 cm and a larger basal area, conditions that are considered to be characteristic of primary forest (Bhat et al., 2000). They preferred to place their nests between the buttresses of large trees (DBH ranging from 63.5 to 359 cm). Similar behavior has been observed for Siamese firebacks in sub-montane forest habitat (Sukumal et al., 2010). Selecting the base of a tree trunk as a neighbouring object for nesting has been reported for other galliform species such as the scaly-breasted partridge (*Arborophila choloropus*) in Khao Yai National Park, Thailand (Ong-in, 2011), Tibetan eared pheasant (*Crossoptilon harmani*) in Lhasa, Tibet (Lu & Zheng, 2003), and Chinese grouse (*Bonasa sewerzowi*) in Lianhuashan, China (Sun et al., 2007). Although nesting between tree buttresses can provide shelter from potential predators by limiting their detection range, we suggest that a disadvantage is that escape flights may be limited when birds face large predators.

Moreover, the models suggested a negative response to predation pressure (Table 4). Siamese firebacks selected a location associated with low predation pressure surrounding the nest-site. Previous studies on nest predators of Southeast Asian evergreen forest birds indicated that predation was the main cause of nest failure, accounting for 91.7% of nest failures (Pierce & Pobprasert, 2013). Natural selection should favor birds that choose habitats that reduce the negative effects of nest predation given the importance of reproductive success to fitness (Martin, 1993). Increased nest predation reduces avian recruitment, limits population growth and can make some populations non-sustainable (Cowardin et al., 1985).

Interestingly, we found that one of the radio-tagged female nested twice (2011 and 2012) in dry dipterocarp forest, fairly close to the edge of the evergreen forest, but outside her normal yearly home range. This seems to be the case in area of fairly high nesting densities which has been reported in previous ring-necked pheasant (*Phasianus colchicus*) studies but failed to explain the direct relationship to the placement of a nest and its distance from the edge of the habitat (Strode, 1941; Nelson et al., 1960).

CONCLUSIONS

Our results are similar to those from previous studies and we provide a larger dataset of nest outcomes for Siamese firebacks in their typical lowland forest habitat. Our results confirm that Siamese fireback significantly prefer to nest in areas associated with higher percentage of ground cover, steep slopes, higher basal area of large trees and low predation pressure. As we found very low nest success, we suggest that further studies are needed to investigate the main causes of nest failure and the main nest predators.

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