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Original research article

Estimating density of secretive terrestrial birds (Siamese Fireback) in pristine and degraded forest using camera traps and distance sampling

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A B S T R A C T

Tropical Asian Galliformes are secretive and difficult to survey. Many of these species are considered "at risk" due to habitat degradation although reliable density estimates are lacking. Using camera trapping and distance sampling data collected on the Siamese Fireback (*Lophura diardi*) in northeastern Thailand, we compared density estimates for pristine and degraded lowland forest. Density was poorly estimated using distance sampling, likely due to small sample size arising from poor visibility in dense vegetation and bird's sensitivity to observers. We analysed camera trap data using both count-based and presence/absence-based methods. Those density estimates had narrower confidence intervals than those obtained using distance sampling. Estimated density was higher in dry evergreen forest (5.6 birds km^{-2}), than in old forest plantations (0.2 birds km^{-2}), perhaps because dense forest habitats provide Firebacks with more resources and refuge from predation. Our results suggest that camera trap data can be used for estimating density of cryptic terrestrial bird species inhabiting tropical forest that lack unique identification markings. However, this technique requires that the effective sampling area is known and thus requires knowledge of the animal home range size.

1. Introduction

Of the c. 300 Galliformes species found worldwide, 26% are classified as "threatened", largely due to habitat loss and degradation, hunting and human disturbance (IUCN, 2013). In tropical Asia, there are 180 species of Galliformes (Madge and McGowan, 2002) of which 21 (∼12%) are of global conservation concern (1 Critically Endangered, 4 Endangered, and 16 Vulnerable species IUCN, 2012). Despite the threats facing tropical pheasants (Phasianidae), little is known about the basic biology of most species. Moreover, many species are secretive and hard to observe, making most traditional bird survey methodology difficult to implement.

Deforestation and habitat degradation in tropical regions represents a major threat to global biodiversity (Laurance and Bierregaard, 1997; Watson et al., 2004). When deforestation occurs, the amount of habitat available of forest species is

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reduced, and the original forest is replaced by plantations or other agricultural uses (Forman, 1995). As forest fragments become smaller, they will be subjected to increased edge effects and human pressure, resulting in habitat degradation (Watson et al., 2001; Beier et al., 2002). Animals occupying degraded forests may face reduced food resources and refuges, and in some cases increased pressure from invasive species (Schwitzer et al., 2011). Consequently, species must respond to changes in dietary composition and diversity, group size and adult sex ratio, and population density (Schwitzer et al., 2011). For birds, studies have suggested that tropical plantations and modified forests can support a variety of taxa including many forest specialists, especially in close proximity to natural forest, and sometimes at higher abundance and richness than in primary habitat (Barlow et al., 2007; Greenberg et al., 1997). In contrast, some studies have argued that the value of such plantations has been overstated (Barlow et al., 2007) and that benefits may only be temporary (Mintra and Sheldon, 1993). Thus, understanding the responses of species to habitat, especially in changes of abundance and density to heavily modified habitat can help to design habitat management and to make strategies for species conservation.

Animal abundance provides the most critical information for defining the status of a species and thus for conservation assessments and practical wildlife management (Conroy and Carroll, 2001). A large number of techniques exist for assessing population abundance and density, including quadrant or plot sampling techniques (Jaeger and Inger, 1994), distance sampling (Thomas et al., 2012; Buckland et al., 2001), photographic mark-recapture methods (Karanth and Nichols, 2002; Karanth et al., 2004), repeated presence–absence surveys (Royle and Nichols, 2003) and repeat count surveys (Royle, 2004). However, each of these techniques makes assumptions that can be difficult to meet for cryptic terrestrial birds such as some Galliformes. Distance sampling requires that the surveyed species should be detected by visual or auditory means (Thomas et al., 2012; Buckland et al., 2001). Applying distance sampling to survey some Galliformes has been previously discouraged, because of the increased probability of not detecting animals on the transect line owing to their cryptic behavior and the possibility that they may be able move quietly away from their initial location before detection (Winarni et al., 2005). Photographic mark-recapture is based on the identification of individuals using unique markings (Karanth and Nichols, 2002). Repeated presence–absence and repeated count survey (Royle, 2004) could provide an alternative method to estimate abundance where identification of individuals in not required. For example, the model described in Royle (2004) has been used to estimate occurrence and abundance of Great Argus Pheasant (*Argus argusianus*) using camera-trap data (O'Brien and Kinnaird, 2008), however, the results indicated a population trend but the accuracy of those estimates were not tested. Moreover, O'Brien and Kinnaird (2008) did not attempt to estimate density as the method is not considered rigorous using camera-trap data.

In northeastern Thailand, Siamese Fireback (*Lophura diardi*) is relatively abundant in some protected areas where it is found predominantly in lowland and foothill forest habitats (<800 m elevation) of mainland Southeast Asia but seams to also tolerate considerable degradation of their forest habitat, such as moderate logging and cultivated field in small clearing (BirdLife International, 2012) and forest regeneration through plantations of *Eucalyptus* and *Acacia* (Suwanrat, 2013). This makes the species an excellent candidate species for quantitatively investigating the effect of habitat degradation on pheasants while testing the efficacy of various survey techniques that could be applied to tropical Asian Galliformes, a group which currently lack a practical field survey method for population estimation due to their secretive behavior (non-calling birds, and inhabiting dense tropical forest).

In this work we focus on a resident Siamese Fireback population in Sakaerat Biosphere Reserve (northeastern Thailand) inhabiting both dry evergreen forest and areas reforested with *Acacia* and *Eucalyptus*. We start by estimating the abundance and density of the species in both habitats (undisturbed dry evergreen forest and disturbed forest plantation) using camera trapping and distance sampling data. Second we assess the different methods by comparing our camera trap and distance sampling derived estimates of abundance and density to estimates based on spot mapping (also known as territory mapping) of radio-tagged Siamese Firebacks. Assuming that spot mapping can be considered closest to "true density", the method/model that provides density estimates closest to those values, with narrow confidence interval can be considered an appropriate approach for estimating Siamese Fireback density.

2. Materials and methods

2.1. Study area

The study was conducted at Sakaerat Environmental Research Station (SERS; Fig. 1), classified as a UNESCO biosphere reserve since 1967. The reserve, covering 78.09 km^2, is located in northeastern Thailand (14° 30′N, 101° 55′E) on the edge of Thailand's Korat Plateau at an elevation of 280–762 m. SERS has two major natural forest types: dry evergreen forest (46.82 km^2) and dipterocarp forest (14.51 km^2), and two large patches of more than 20 year old forest plantation of mixed acacia (*Acacia spp.*) and eucalyptus (*Eucalyptus spp.*, 14.46 km^2), and several small patches of bamboo forest (1.12 km^2), grassland (0.93 km^2) and the office and operational building (0.25 km^2) (Thailand Institute of Science and Technology, 2012a). Average annual precipitation is 1071 mm with a dry season from November to April (average monthly rainfall of 210 mm) and a wet season from May to October (average monthly rainfall of 860 mm). Average annual temperature is 26.1 °C (ranging from a low monthly average of 19.3 to a high of 32.8 °C) and the average relative humidity is 82.2% (monthly range of 74%–87%) (Thailand Institute of Science and Technology, 2012b).

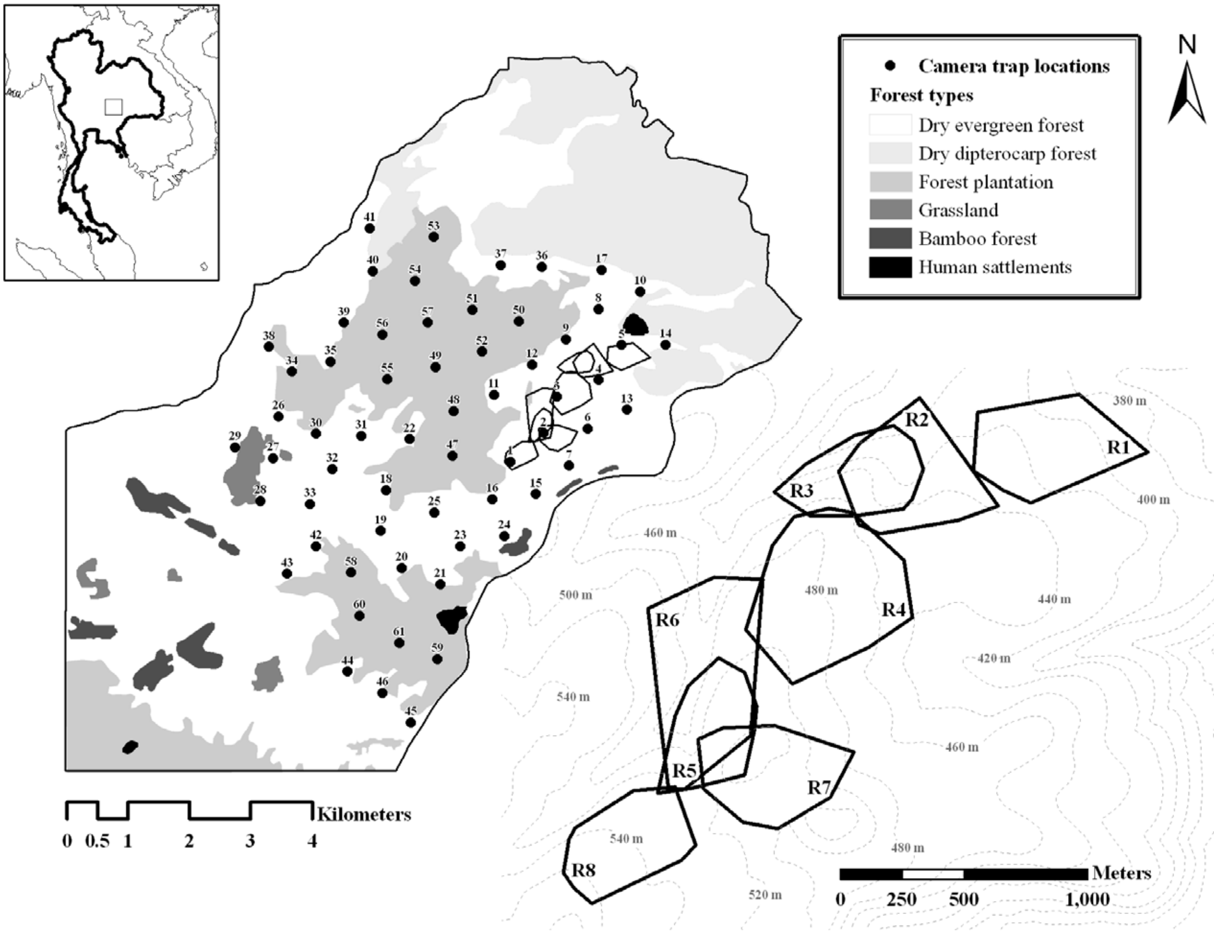

Fig. 1. The location of the Sakaeret Environmental Research Station in Nakhon Ratchasima, Thailand. The 61 locations of camera trap are shown using numbered black filled circles. Calculated 95% minimum convex polygons based on telemetry are shown for the eight Siamese Fireback groups (solid black line polygons, R1–R8).

2.2. Study species

Siamese Firebacks live in groups with a dominant male and sometimes with subordinate that monopolises all females in the group during both the breeding and non-breeding seasons. Other social units reportedly include floaters – solitary males excluded by a stable group – or in a few cases a pair of floaters (Savini and Sukumal, 2009). The breeding season is February until July, with mating occurring in February to April and nesting in April to July. Females do not nest synchronously (Savini and Sukumal, 2009). Floaters can be observed during January and February, the period that animals travel long distances to look for breeding opportunities (Savini and Sukumal, 2009).

2.3. Camera trapping

Camera trap surveys were conducted during the 2011 breeding season (February to May) when, on the basis of our observations, birds are more active. Camera-traps were mounted on tree trunks at a height of 45 cm at 61 randomly selected camera locations in two forest types; 46 in dry evergreen forest (DEF) and 15 in old forest plantation (OFP) (Fig. 1). Assuming that an individual would need to come into direct contact with a camera, and using the 0.30 km^2 home range size reported by Sukumal et al. (2010) in a study of a sub-montane population of Siamese Fireback we placed cameras 700 m apart (i.e. approximately the diameter of a circular home range of 0.30 km^2 which is 618 m). Such trap spacing allows for some local variation in home range size while avoiding violation of the assumption that animals should not be detected at more than one site. We used passive infrared camera traps with flash (Stealth Cam, TX, USA) with the date and time stamp on each photograph. Cameras were programmed to run continuously (24 h a day) for 14 days at each camera location and to take nine consecutive pictures per trigger with one minute delay between triggers. Each trap was baited with rice once at the same time to maximise capture. We identified each photo with a Siamese Fireback, recorded the time and date of the photograph, and counted the number of individuals in each photo. To reduce the chance of double counting of individuals making multiple passes of the cameras, and thus the potential to overestimate abundance, we considered only photographs taken in a one hour window that corresponded to the peak period of activity each day; between 0630 and 0730. We used each day of the 14 camera trapping days as replicate occasions which yielded both repeated count data, the number of Siamese Fireback individuals detected in each day, and repeated presence–absence data, whether or not at least one Siamese Fireback individual was detected in each day. To investigate habitat suitability, we estimated habitat specific abundances dry evergreen forest (DEF) and old forest plantation (OFP).

To estimate Siamese Fireback abundance from camera trapping data, we fitted two types of model for estimating abundance: the Royle–Nichols model using repeated presence–absence data (Royle and Nichols, 2003), and the binomial mixture model using replicated count data (Royle, 2004). These models assume that the probability of detecting an animal at a site is a function of the number of animals at that site and that the detection of one bird at a site is independent of the detection of any other birds (Royle, 2004). However, Siamese Firebacks are gregarious, violating this assumption because the detection of one group member is likely to be related to the detection of other group members. To account for this non-independence in detection, we fitted a beta-binomial mixture model (Martin et al., 2011) to the repeated count data.

The Royle–Nichols model was fitted using the "unmarked" package (Fiske and Chandler, 2011) implemented in program R version 3.0.1 (R Development Core Team, 2011). Each of the candidate models were ranked using Akaike Information Criterion (AIC; Akaike, 1973) and model fit was assessed using parametric bootstrap of the chi-square goodness-of-fit statistic (1000 iterations). We then fitted the binomial mixture model and the beta-binomial mixture model using JAGS program version 3.3 (Plummer, 2003) run from R via the "R2jags" package (Su and Yajima, 2012). Vague, uninformative priors were used for all parameters in both models. The posterior parameter estimates are based on a Markov chain Monte Carlo (MCMC) analysis with three separate chains of 50,000 iterations (the first 5000 were discarded as a "burn in"). Model convergence was assessed using the Rhat value, where a value close to 1 indicated convergence (Gelman and Hill, 2007). Goodness-of-fit was evaluated for both models using Bayesian P-value based on chi-squared discrepancy (Gelman et al., 2004), where a Bayesian P-value close to 0.5 indicates that a model appears to fit the data.

To convert estimates of Fireback abundance to density, we divided the estimated (habitat specific) population size (N) by the effective sampling area of the camera traps. As is standard practice in camera trapping studies, we calculated the effective sampling area based on the average home range size (Karanth and Nichols, 1998; Soisalo and Cavalcanti, 2006). We here used our telemetry data to estimate home range size and we calculated the effective sampling area as being a circular buffer around each camera with a radius equal to the diameter of the average home range (or a diameter of $2d$). Using the "Proximity" analysis tool in the ArcGIS version 9.3 (ESRI, 2009) habitat (forest) specific buffer polygons were created, removing any overlap, allowing habitat specific densities to be calculated. Average home range size was estimated using data collected from radio-tagged individuals from a concurrent telemetry study of Firebacks in the study area (see Telemetry section below).

2.4. Distance sampling

Distance sampling was also conducted between February and July 2011. We established 61 line transects, all 200 m long, each intersecting a camera trap location. Transect surveys were conducted 1–2 days after camera traps were set up at each location. A pair of researchers (observer and protected area staff) walked the transects at an average speed of 20 m min^{-1} between 0700 to 1000 and 1400 to 1700, times we considered to be highest Siamese Fireback activity. Transects were walked 4–5 times per site mostly at the same time as the camera traps were operated. However, to increase the number of detections in OFP, we additionally walked transects a further 5 times in two months after the cameras were deactivated. In total, 73.8 km was walked (43.8 km in DEF and 30.0 km in OFP). For each group visually encountered while walking the transects, we recorded the number of individuals in the group and the perpendicular distance of the group from the transect.

We used program DISTANCE version 6.0 (Thomas et al., 2009) to estimate detection probability and density of Siamese Fireback using conventional distance sampling (CDS). AIC was used to select the appropriate combination between the four commonly used key detection functions (uniform, half-normal, hazard-rate and negative exponential) and adjustments (cosine terms, Hermite or simple polynomials). The occurrence of Siamese Firebacks in groups is likely to influence detectability in dense forest: specifically, birds in large groups tend to be easier to detect than smaller groups and the geometric center of the cluster when part of group membership might be unseen can be difficult to determine. When smaller clusters are more likely to be detected at shorter distances, average cluster size is likely to be overestimated. We used the size-bias regression method within program DISTANCE to account for, and estimate expected cluster size (Buckland et al., 2001).

2.5. Telemetry

The study area of telemetry is dominated by dry evergreen forest at elevations ranging between 350 and 580 m. Siamese Firebacks were caught using mist nets (Keyes and Grue, 1982) and modified traditional leg snares made from bamboo and soft polyester string (Schemnitz et al., 2009) between April 2010 and February 2011 ($n = 6$) and then again in November and December 2011 ($n = 2$), a period that overlapped with both the camera trapping and distance sampling surveys. All birds caught were banded with a unique combination of two or three coloured and one metal band (11A size, Thai Royal

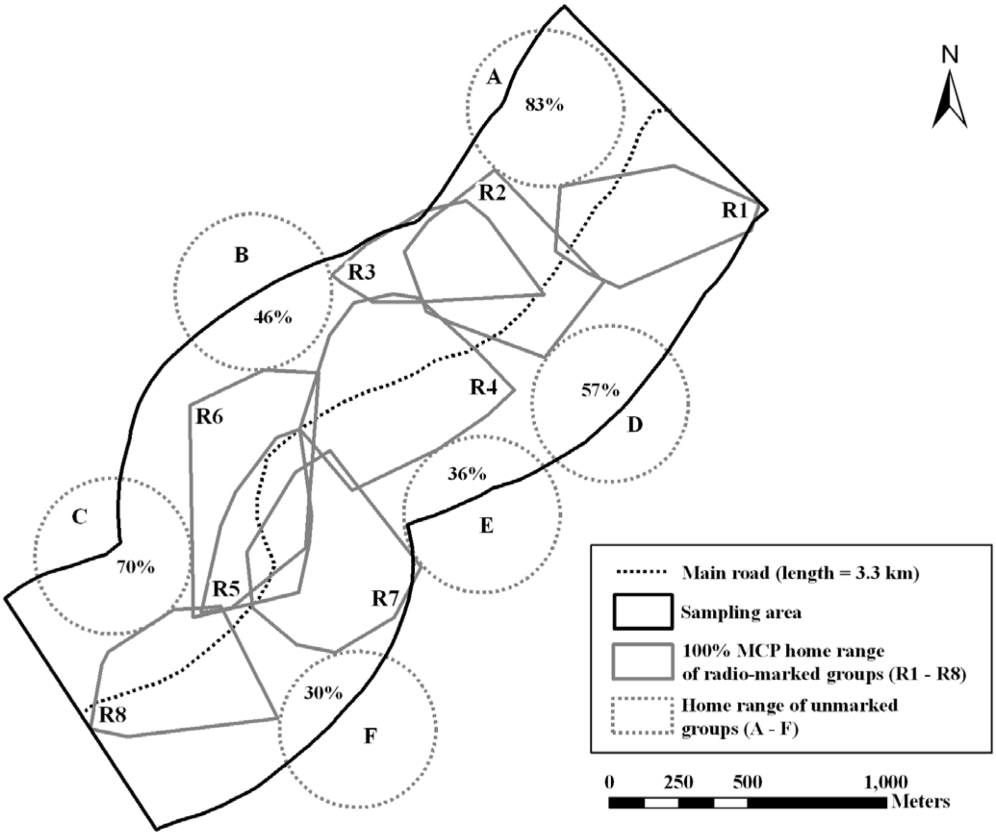

Fig. 2. Spot mapping of Siamese Firebacks in the study area. Total of 14 groups, including eight radio-marked groups (gray line polygons, R1–R8) and six other groups (dash line polygons, A–F) were found in the sampling area of 3.3 km^2. Percentages indicated home range overlapping the sampling area of the six other groups.

Forest Department). Each captured bird was fitted with a 15 g necklace-type radio-transmitter (model RI-2B, Holohil System Ltd.) with a life span of approximately 24 months. Birds were located by homing on average every two days using ATS R410 receivers and three-element Yagi antennae. We recorded the location of the birds, using a global positioning system (GPS) unit, and the size and composition of the group. Home ranges were estimated using standard minimum convex polygons (MCP). We estimated 95% MCP to calculate home range size and used the Animal Movement Extension (Hooge and Eichenlaub, 1997) in Arcview 3.2a (ESRI, 1999) to estimate home range overlap.

To estimate density using spot mapping (Bibby et al., 2000), we determined the sampling area 3.3 km^2 from intensive tracking area of radio-tagged birds. The sampling area was bisected by the main road (length = 3.3 km) with tracking buffer width equal to the maximum distance from transmitter to receiver (500 m) on both sides of the road. Groups of birds without radio-tags inside and outside of the sampling area were also recorded. We estimated 100% MCP of all radio-tagged birds that remained completely within the sampling area. The average home range from all radio-tagged groups was used as a home range size of additional (untagged) groups that observed in the sampling area. The additional untagged groups were not confident in determine their group size and how much their ranges overlapping with other groups. We added additional groups of untagged birds and quantified the proportion of circular ranges that were inside the sampling area (groups A–F with dashed circular home range in Fig. 2). We determined the size of unmarked groups (i.e. groups with no tagged individuals) based on the proportion inside the sampling area compared to mean group size, minimum and maximum of radio-tagged groups (Elbroch and Wittmer, 2012; Rinehart et al., 2014). For example, the group size of a group with a home range that lies 50% inside the study area is 0.5 $\times$ mean group size. Density estimates were obtained from the total number of individuals found divided by the sampling area.

3. Results

3.1. Camera trapping

Siamese Firebacks were detected in 16 of the 61 camera locations (15 in DEF and 1 in OFP). We obtained 49 independent events of Siamese Firebacks (48 events in DEF and 1 event in OFP) with a total sampling effort of 808 trap-nights (average

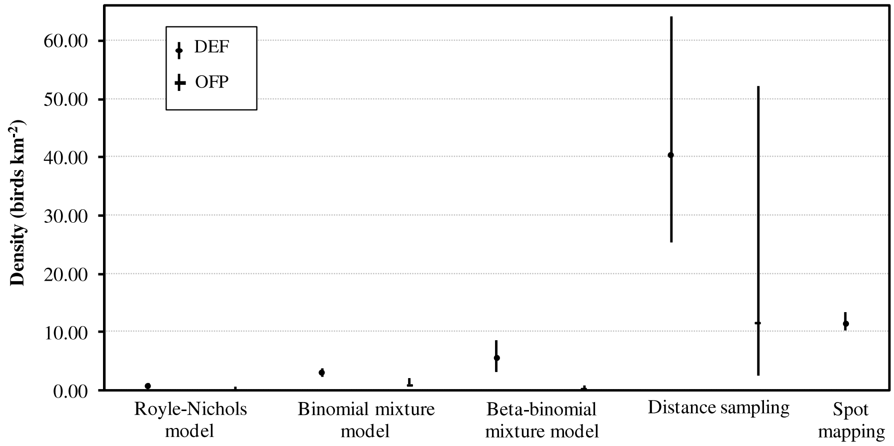

Fig. 3. Density estimates (±95% CI) of Siamese Firebacks in dry evergreen forest (DEF) and old forest plantation (OFP) based on camera trapping, and distance sampling. The telemetry data was mean, minimum and maximum of the estimates.

13.3 ± 0.2 (SE) nights location^{-1}). Based on our telemetry data, the average 95% MCP home range size of Siamese Fireback during breeding season was 0.21 ± 0.02 (SE) km^2 (see Telemetry results below). The diameter of a circular home range of this size is 514.4 m giving a total effective sampling area of 39.50 km^2, 29.16 km^2 in DEF and 10.34 km^2 in OFP.

Using the Royle–Nichols model, a model with habitat specific Fireback abundance received most support (88% of the model weight based on AIC). The bootstrapped chi-square goodness-of-fit test indicated that the model adequately explains these data ($P = 0.58$). We then fitted binomial mixture and beta-binomial mixture models to the count data to estimate habitat specific abundance. Comparing the Bayesian P-values (0.00 vs. 0.53) and the lack of fit ratio (2.93 vs. 0.98) of the beta-binomial mixture model and the binomial mixture model respectively suggests the beta-binomial mixture model provides a better fitting model to the data.

The estimated detection probability based on repeated presence–absence data (Royle–Nichols model) was higher than those estimates based on replicated count data (binomial and beta-binomial mixture model), while the estimated site abundance was lower (Table 1). The estimates of habitat specific abundance indicated higher Siamese Fireback abundance in DEF compared to OFP (Table 1 and Fig. 3).

Utilising the mean estimated habitat specific abundance and confidence interval derived from the model estimates using Royle–Nichols model, binomial and beta-binomial mixture model multiplied by 46 camera locations in DEF, and the effective sampling area in DEF equal to 29.16 km^2, we obtained the density estimates of 0.77 birds km^{-2} for Royle–Nichols model, 3.00 birds km^{-2} for binomial mixture model, and 5.60 birds km^{-2} for beta-binomial mixture model (Table 1 and Fig. 3).

3.2. Distance sampling

We recorded a total of 31 detections; 23 detections in DEF sites and 8 detections in OFP sites. Because of our small sample size, fitting the detection function with different level of truncation produced estimates with large uncertainty (wide confidence interval) and large coefficient of variance (%CV > 50%). Thus, we analysed the data using the size-bias regression method. Using only data from DEF sites, the uniform distribution with a cosine adjustment term and estimating cluster size based on a size bias regression method (Buckland et al., 2001) produced the best detection function fitting our data based on AIC. The observed cluster size ranged from one to seven. The estimated of expected cluster size E(s) from regression method was 2.7 birds group^{-1} (95% CI = 2.1–3.7). Siamese Firebacks were detected with the probability of 0.56 and the effective strip width was 17.9 m. Estimated density was 40.3 birds km^{-2} (%CV = 23.6%, 95% CI = 25.4–64.1; Table 2 and Fig. 3).

Using only data from OFP sites, we only fitted the detection function with three different key functions because the uniform distribution was considered unreliable due to small sample size and so it was excluded from this analysis. The results showed that the negative exponential distribution with a cosine adjustment term produced the best model fit based on AIC. Cluster size ranged from one to five, with a mean cluster size of 2.1 birds group^{-1} (95% CI = 1.6–2.9). Siamese Firebacks were detected with the probability of 0.99 which can be considered unreasonable and most likely the result of a small sample size ($n = 8$). The effective strip width was 24.3 m. Estimated density was 11.7 birds km^{-2} (CV = 78.7%, 95% CI = 2.6–52.2; Table 2 and Fig. 3).

3.3. Telemetry

A total of eight Siamese Firebacks were caught and fitted with radio collars and each bird representing a distinct group. Birds were located on average in 86.0 ± 1.7% of tracking attempts (range 78.4%–91.5%). The average 95% and 100% MCP home range size during breeding season were 0.21 ± 0.02 (SE) km^2 and 0.25 ± 0.02 (SE) km^2 (Table 3). Based on 95%

Table 1
Estimated probabilities of detecting an animal (p) and site abundance (λ) with their lower and upper 95% confidence interval (CI) from the Royle–Nichols model (presence–absence based model), binomial mixture model and beta-binomial mixture model (count based models).

Model	Detection probability (p)		Site abundance (λ, birds site^{-1})				Density (birds km^{-2})			
			DEF		OFP		DEF		OFP	
	Estimate ± SE	95% CI	Estimate ± SE	95% CI	Estimate ± SE	95% CI	Estimate ± SE	95% CI	Estimate ± SE	95% CI
Royle–Nichols model	0.16 ± 0.03	0.11–0.23	0.49 ± 0.13	0.25–0.73	0.07 ± 0.07	0.01–0.40	0.77 ± 0.22	0.39–1.25	0.10 ± 0.10	0.01–0.58
Binomial mixture model	0.14 ± 0.02	0.11–0.17	1.90 ± 0.04	1.44–2.45	0.08 ± 0.02	0.00–0.29	3.00 ± 0.06	2.27–3.86	0.12 ± 0.03	0.00–0.42
Beta-binomial mixture model	0.06 ± 0.01	0.04–0.09	3.55 ± 0.13	1.98–5.50	0.14 ± 0.04	0.01–0.53	5.60 ± 0.20	3.12–8.68	0.20 ± 0.06	0.01–0.77

Table 2
Results of density estimates in different habitat types, dry evergreen forest (DEF) and old forest plantation (OFP) using distance sampling.

Habitat	n	L	μ	$\bar{s}$	P	$\widehat{D}$	% CV	95% CI
DEF	23	43.8	17.9	2.7	0.56	40.3	23.6	25.4–64.1
OFP	8	30	24.3	2.1	0.99	11.7	78.7	2.6–52.2

Note: n = number of cluster seen (cluster), L = total length of transect walked (km), μ = the effective strip half-width (m), $\bar{s}$ = the mean sample cluster size (birds cluster^{-1}), P = detection probability, $\widehat{D}$ = estimate density of birds km^{-2}, CV = the coefficient of variance, CI = confidence interval.

Table 3
Means ($\pm$ SE) of the number of radiolocations, percentage of radio-tracking success, 95% and 100% minimum convex polygon (MCP) home range size (km^2) and group size of Siamese Firebacks during breeding season in Sakaerat Environmental Research Station, Nakhon Ratchasima, Thailand.

Group	Number of radiolocations	Percentage of radio-tracking success (%)	95% MCP Home range size (km^2)	100% MCP Home range size (km^2)	Group size (birds)
R1[a]	39	89.7	0.20	0.22	4
R2[b]	47	91.5	0.21	0.28	3
R3[a]	33	90.9	0.15	0.17	4
R4[a]	35	85.7	0.32	0.33	2
R5[a]	44	86.5	0.15	0.17	5
R6[b]	51	78.4	0.30	0.33	3
R7[a]	50	80.0	0.19	0.29	2
R8[a]	44	85.0	0.16	0.22	4
Average	42.9 $\pm$ 2.4	86.0 $\pm$ 1.7	0.21 $\pm$ 0.02	0.25 $\pm$ 0.02	3.4 $\pm$ 0.4

[a] Using tracking data and observing during February and May 2011.
[b] Using tracking data and observing during February and May 2012.

MCP home ranges, the average overlap area between two neighboring groups was 0.03 $\pm$ 0.01 (SE) km^2 and among three neighboring groups was 0.01 $\pm$ 0.01 (SE) km^2 (Fig. 1). Group sizes during these periods were found ranging from two to five birds with the average group size of 3.4 $\pm$ 0.4 (SE) birds group^{-1} (Table 3).

Within the sampling area of 3.3 km^2 (7% of total DEF area), 14 groups were observed; eight were groups containing tagged individuals (R1–R8, Fig. 2), and six were "unmarked" groups (A–F, Fig. 2). We observed 27 birds from all radio marked groups that remained completely within the sampling area. Percentages of home range overlapping the sampling area of the six other groups range from 30% to 83% (Fig. 2). Using the average group size of 3.4 birds group^{-1} (min. = 2, max. = 5), we obtained 11 birds (min. = 7, max. = 17) from the additional six groups. In total, 38 birds (min. = 34, max. = 44) were observed in the census area. The density was 11.5 birds km^{-2} (min. = 10.3 birds km^{-2}, max. = 13.3 birds km^{-2}, Fig. 3).

4. Discussion

Siamese Fireback density was higher in pristine dry evergreen forest than in disturbed forest plantation when we applied both distance sampling and the analysis of camera trap data using the Royle–Nichols, binomial and beta-binomial mixture models. When comparing the three survey methods (spot mapping, distance sampling and camera trapping) using the beta-binomial mixture model for the camera trap data provided the more precise density estimate as it accounts for both imperfect and non-independent detection of elusive and gregarious animals. Although converting estimates of abundance derived from camera trapping data requires a definition of the effective area sampled, we were able to calculate it using direct estimates of home ranges of telemetered individuals. Direct estimates of density using distance sampling methods were poorly estimated, most likely due to small sample size, lack of visibility in (preferred) dense vegetation and the bird's extreme sensitivity to observers. Given the ability to incorporate knowledge of the species behavior (elusiveness and gregariousness), the availability of estimated home ranges from tracked individuals in the study area, and the precision of abundance estimates, we suggest that analysing camera trapping data using beta binomial mixture models is an appropriate method for estimating density of Siamese Firebacks.

4.1. Habitat preference of Siamese Fireback

Estimates of Siamese Fireback density were higher in DEF than in OFP regardless of methodology used. Our results suggest that habitats with dense understory vegetation are more suitable for Siamese Firebacks, most likely because of higher food availability but also as a strategy to reduce predation risk. Many species, including Galliformes, tend to use areas with dense understory vegetation which provides good shelter when raising chicks as the mortality of young chicks is high in the first few weeks (Lima, 1993; Peh et al., 2005). Such patterns of habitat preference are shown by male Sichuan Hill Partridges (*Arborophila rufipectus*) in southern China (Liao et al., 2008) and Hume's Pheasant (*Syrmaticus humiae*) in northern Thailand (Iamsiri and Gale, 2008).

Many studies, however, suggest that plantation forests can have a relatively high biodiversity value (Duran and Kattan, 2005). For example, coffee plantations can play an important role as refuges and breeding habitats for a variety of bird species in the Western Ghats, India (Shahabuddin, 1997); Peh et al. (2006) mentioned that rubber tree plantations can act as corridors that increase the connectivity between forest remnants for forest species persisting in agricultural landscapes; and Round et al. (2006) suggested that if the undergrowth beneath forest orchards was allowed to grow, the population of some understory birds might increase. Anecdotal observations of Siamese Firebacks in our study area during the past few years have indicated a potential range expansion from their natural habitat (DEF) to plantation habitat (Suwanrat, 2013). However, despite the reforestation program having started in 1982, our estimates of density in OFP habitats was markedly lower than in DEF suggesting that OFP is sub-optimal habitat.

4.2. Comparison of methods

Our reference point when comparing the accuracy of different survey methods is linked to the density estimates obtained using spot mapping. Spot mapping has been widely accepted as an accurate method for measuring absolute abundance of bird territories in a given area (Bibby et al., 2000). Although Siamese Firebacks are not territorial birds, during the breeding season the species has a relatively well defined home range and overlap for which the number of groups defined in the sampling area is precise. Moreover, the total number of birds in each group that were observed with radio-tagged birds over a relatively long period of time was also known. We assume therefore that estimates of group and bird density based on spot mapping can be considered close enough to "true density" estimate.

Comparing estimates of Siamese Fireback density based on two different data collection techniques, camera trapping and distance sampling, is non-trivial because in distance sampling, the effective area sampled (i.e., the strip width), is estimated and therefore, density is directly computed (Buckland et al., 2001). To estimate density using camera trap, density is entirely determined by the definition of the effective sampling area (Royle et al., 2013). However, the concurrent telemetry study of eight individuals within the study area allowed for the estimation of average Siamese Fireback home range sizes, providing a reasonable measure of the effective sampling area, i.e. a circular buffer with a radius equal to the diameter of the average home range. Although MCP methods have been shown to over-estimate home range size when compared with fixed kernel methods, when sample size was small, as is the case in our study, MCP produces more accurate estimates of home range size (Arthur and Schwartz, 1999; Boyle et al., 2008; Taft et al., 2008). Estimates of density based on camera trapping data (RN, binomial, and beta-binomial mixture models) were all lower and closer to spot mapping density estimates (i.e., more accurate) than those derived from distance sampling, and they were always more precise (i.e., had narrower confidence intervals, Fig. 3). We acknowledge that we do not know the "true" model, although, it is encouraging that analysis of the camera trapping data using the binomial mixture models allowed enough flexibility so as to incorporate our biological knowledge about Siamese Firebacks and potential assumption violations into the model.

The performance of density estimation using distance sampling depends largely on the behavior of the target species (Gale et al., 2009) as well as survey specific factors such as the time of survey, weather, bird activity and their susceptibility to being counted (Bibby et al., 2000). The imprecision in density estimates from our distance sampling data relative to the analysis of camera trap data is therefore unsurprising given that Siamese Firebacks are cryptic, not particularly vocal, and prefer dense forest habitat, all contributing to small sample sizes. Such limitations have been discussed in other studies that suggest distance sampling will underestimate population size for some tropical forest birds when compared with densities derived from territory mapping of colour banded birds (Gale et al., 2009), and in dune-dwelling lizards where the assumption of perfect detection of individuals on the transect line was violated (Smolinsky and Fitzgerald, 2010). An additional limitation when using distance sampling to estimate the density of secretive, group living and ground dwelling birds is that, although larger groups are easier to detect and group size may be accurately estimated close to the line, group sizes are poorly estimated at greater distances (Buckland et al., 2008) which is likely to have led to the underestimation of not only group size, but also the perpendicular distance from the observer to the center of a group (e.g. Brugiere and Fleury, 2000). Our study is consistent with these suggestions and confirms the need to consider carefully both the study design and species behavior prior to carrying out distance sampling.

We compared three models for estimating density using data collected from camera traps; the Royle–Nichols model, the binomial mixture model and the beta-binomial mixture model, all of which used the same effective sampling area as the unit to convert abundance to density (effective area sampled $= 39.50$ km^2). Density estimates from each of the models are broadly comparable. First the Royle–Nichols produces lower estimates of abundance (and hence density) as it is based on presence–absence data only and do not use groups size. Second, the binomial N-mixture models is a count based model (it retain information on group size) but does not account for non-independent detections (Martin et al., 2011) resulting in better density estimates. In the end, the beta-binomial model provided the more accurate density estimates as, besides using count data it also account for non-independent detections. Based on the advantages and disadvantages of the different methods our study suggests that camera trapping data analysed using beta-binomial mixture models is a suitable alternative to distance sampling, especially for monitoring cryptic, ground dwelling and gregarious species such as tropical Asian Galliformes.

The use of camera traps and associated abundance models does however require careful consideration regarding violation of model assumptions and the need to define the effective sampling area when converting estimates of abundance to density. Our use of the beta-binomial model reflected directly our knowledge of the gregarious behavior of Siamese Firebacks (see above). However, an additional concern is that the presence of transient individuals can result in the violation of the assumption that animals should not be detected in more than one site (Sutherland et al., 2013) because these floaters can be detected at consecutive camera trap sites resulting in an overestimate of abundance. The mating strategy observed in this species; dominant males stay in close proximity to females while subordinate males move as isolated floaters (Savini and Sukumal, 2009) may explain the observation of a relatively high frequency of solitary males and male groups (''floaters'') in our study. This is consistent with a previous study of a sub-montane population of Siamese Firebacks in which high numbers of floaters were observed during January and February (Savini and Sukumal, 2009). When transients are suspected in the population, our recommendation is to restrict the sampling window to one hour as we did (i.e. 0630–0730) to at least minimize the potential for double counting of large ranging individuals although there may still be bias induced by the presence of floaters. Ideally, observations of a larger number of unique individuals than the number telemetered could be used to estimate movement patterns and density directly using spatially explicit models as suggested by Borchers and Efford (2008) although when individuals lack unique identifying features/marks this can be difficult. In summary, our approach to estimating density using camera trapping data and the beta-binomial model offers a conservative approach for monitoring.

4.3. Effectiveness of camera traps for surveying cryptic terrestrial birds

We have demonstrated the value of camera traps for surveying certain Galliformes. Specifically, data collected using cameras can be used to obtain relatively precise density estimates compared to distance sampling methods. However, care must be taken when using the camera trapping methods to estimate the density of a species in which individuals are not identifiable. It is particularly important to obtain information on home range size in order to determine the appropriate effective area sampled by the cameras. In order to avoid biases in estimates of abundance and density, camera trapping studies need to be designed and applied with a practical knowledge of species' biology and behavior in mind. Camera traps have the potential to obtain improved accuracy in species identification, cause little environmental disturbance, can be used to monitor nocturnal and diurnal species and offer the possibility of studying activity patterns, habitat use and importantly, they require very little operational training (Silveira et al., 2003).

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