Agr. Nat. Resour. 56 (2022) 645–656

AGRICULTURE AND NATURAL RESOURCES

Journal homepage: http://anres.kasetsart.org

Effects of gap age on understory bird population in Mae Sa-Kog Ma Biosphere Reserve, Northern Thailand

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Article Info

Article history:
Received 14 March 2021
Revised 27 February 2022
Accepted 25 April 2022
Available online 30 June 2022

Keywords:
Ecological succession,
Hill evergreen forest,
Monitoring,
Permanent plot

Abstract

Importance of the work: It is important to understand the ecological effects of gap age on the understory bird populations in the conservation of montane forest.

Objectives: To study bird populations in permanent plot in Mae Sa-Kog Ma Biosphere Reserve, Northern Thailand

Materials & Methods: Birds were sampled using mist-netting at 12 gap sites during 5 yr.

Results: In total 1,813 individual birds were caught, representing 82 species, with 330 individual birds recaptured in 38 species, which were classified into three avian feeding guilds. Insectivore were the most abundant guild for both natural gap and closed canopy sites. Frugivorous and nectarivorous birds were prevalent in gaps.

Main finding: Frugivore and insectivore feeding guilds increased over time but did so more rapidly in forest gaps than closed-canopy habitats. The detection probability of birds was higher in forest gaps and increased more quickly in gaps than in closed-canopy habitat, possibly due to gap succession. Forest gaps may function as keystone habitats for birds in their role of sustaining frugivores and nectarivores during periods of fruit scarcity in the forest.

Introduction

Forests are renewable resources that are regenerated by the creation of canopy gaps (Zhu et al., 2014; Yang et al., 2017; Mazdi et al., 2021). Natural or human disturbance of the forest structure alters ecosystem processes and the microclimate of the layers above in turn influences natural regeneration (De Frenne et al., 2021; Hammond and Pokorný, 2021). The appearance of gaps in the forest canopy is important because it begins the forest growth cycle (Whitmore, 1989; Sapkota and Odén, 2009). Gaps are essential for the regeneration of rainforest tree species and are a unique microenvironment (Muscolo et al., 2014). Light quantity changes with gap age and

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https://doi.org/10.34044/j.anres.2022.56.3.19

size, both of which influence natural regeneration (Babweteera et al., 2000).

Gaps created by natural tree fall are essential for creating habitat in forest dynamics. They influence the abundance and distribution of bird species by maintaining habitat heterogeneity, which affects the abundance and distribution of food resources, promoting high biodiversity and providing alternative sites for use by understory birds (Blake and Hoppes, 1986; Restrepo and Gomez, 1998; Rosely et al., 2007; Siri et al., 2019; Lewandowski et al., 2021). Forest gaps provide important resources for many woodland bird species. Many understory birds use forest gaps. For example, Perkins and Wood (2014) suggested that conserving Cerulean Warblers (*Setophaga cerulean*) will require creating small forest gaps (< 100 m^2). This species avoids large clearings because of declines in nesting success resulting from predation and parasitism (Melinda et al., 2012).

Tropical forest loss and degradation are among the most critical environmental issues faced on Earth and in particular, habitat changes due to forest loss and degradation significantly affect bird dispersal ability are among the greatest threats to biodiversity. For example, Symes et al. (2018) investigated 308 forest-dependent bird species and reported that 89% of the species experienced average habitat losses. Siri et al. (2019 investigated only species composition and feeding guilds and compared morphological traits of the legs of understory birds in forest gaps with under-closed canopy habitats. Therefore, in this study, we aimed to investigate the effects of gap age on the population of understory birds and spatial variation in detection probability between forest gap and closed canopy differences in species and guilds that are affected by tree fall and to determine whether the effect corresponded to the use of natural gap versus closed canopy.

Materials and Methods

Study area

A 16 ha permanent plot of lower montane forest in the Mae Sa-Kog Ma Biosphere Reserve (18°48′45.7″N, 98°54′7.7″E) in Doi Suthep-Pui National Park, Northern Thailand (Fig. 1) was the study site. The elevation in the permanent plot was in the range 1,250–1,540 m above mean sea level. The lowest average annual rainfall in the dry season (November to April) was 10 mm, whereas the mean rainfall in the wet season (May to October) was 335.2 mm. Monthly temperatures averaged 18.93–21.79 °C during the wet season and 14.79–22.35 °C in the dry season (Pimrat, 2016). This lower montane forest contained 189 plant species, with a top canopy height of 40 m and the Lauraceae was the dominant family (Marod et al., 2014). The dominant bird feeding guild was foliage-gleaning insectivores, including the Grey-cheeked Fulvetta (*Alcippe morrisonia*), Grey-throated Babbler (*Stachyris nigriceps*), Buff-breasted Babbler (*Pellorneum tickelli*) and Martens's Warbler (*Seicercus omeiensis*) (Siri et al., 2013, 2019).

Bird sampling

Forest gap size was measured in the field according to procedures laid out by Runkle (1992). The sampling protocol was constructed by locating and measuring two perpendicular lines in each gap, with the length (L) being the longest distance within the gap and the width (W), the greatest distance perpendicular to the length. Understory birds were sampled using mist-netting in 12 gaps located in the understory vegetation layer because understory birds are sensitive to habitat change (Barlow et al., 2006; Hatfield et al., 2018; Tchoumbou et al., 2020). Two different habitat types were selected for net placement based on physiognomies: forest gap and closed canopy (Siri et al., 2019; Ponpithuk et al., 2020). All gaps had resulted from natural, large trees falling in the forest canopy and large-scale disturbances to the canopy opening following fires, wind storms, insect outbreaks or tree death (Richards, 1996; Desouza et al., 2001; Muscolo et al., 2014). The closed canopy sample sites were established under continuous forest canopy and initially were separated from the nearest gap by at least 10 m. Two mist nets (each 9 m in length) were set at each net site to provide a total length of 18 m. Nets were arranged in various configurations (at right angles, T-shaped, L-shaped or straight line) to fit within gaps; nets in understory sites were set to match these configurations. All nets in forest gaps were set to 9 m height and nets in the closed canopy were set to 4 m height and contained four shelves. Birds sampling was first performed in October 2014 and then every month for 60 mth until October 2019.

The nets were opened at dawn (0600 hours), checked every 30 min and closed at dusk (1600 hours) with the exception of the hazard weather conditions (Wunderle et al., 2005; Khamcha and Gale, 2012; Werema, 2015; Siri et al., 2019; Ponpithuk et al., 2020). The mist nets were set monthly, with nets opened at four sites per day for three consecutive days (42,480 net-hours). All birds were identified to the species level and age and sex were determined where possible. New

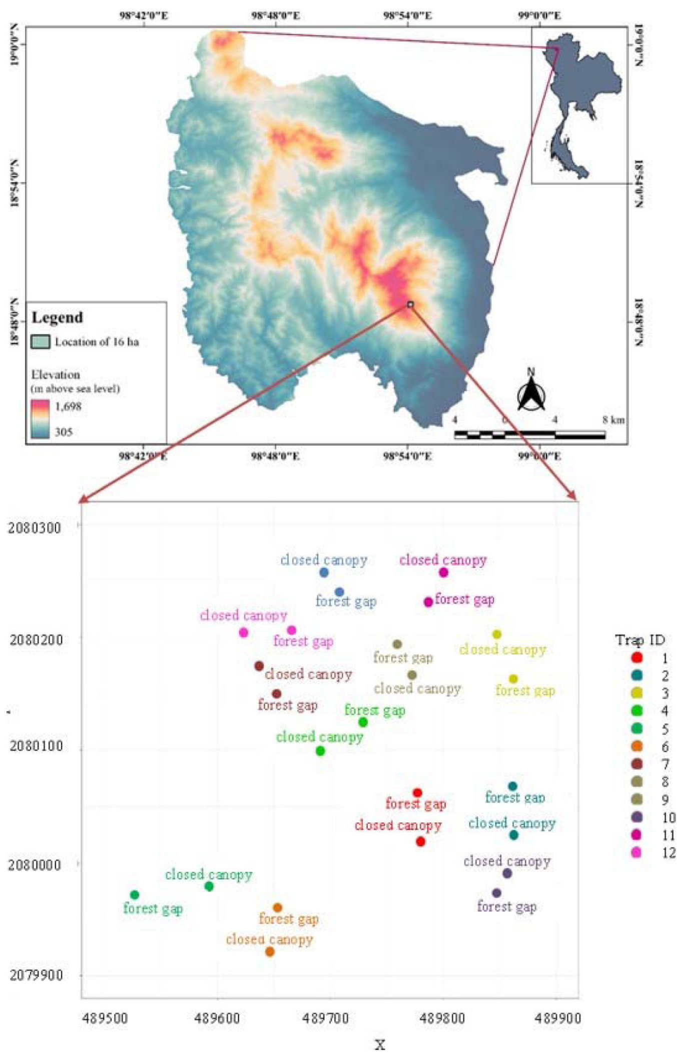

Fig. 1 Location of mist-nets at 12 different sites in a 16 ha permanent plot at Mae Sa-Kog Ma Biosphere Reserve, Thailand where different colors represent mist-net sites

captures and recaptures were recorded. All captured birds were banded using a numbered aluminum ring supplied by the Department of National Parks, Wildlife and Plant Conservation of Thailand, which granted permission for the study (no. DNP 0907.4/9819); captured birds were released in the vicinity of capture.

The birds were classified into four feeding guilds: nectarivores, insectivores, frugivores and carnivores (Wielstra et al., 2011). Carnivores were excluded from the analysis because only one was caught.

Data analysis

Bird species were grouped into two habitat-use associations following Siri et al. (2019).

The spatial patterns were investigated of detection probability of avian understory habitat use in the closed canopy and forest gaps by testing for differences in the associations' total detections, numbers of detections by species, and habitat association according to the gaps, occasions and their interaction. The detection probability is the number of individuals detected to estimate population size changes over time or to estimate density, detection and space use. (Nichols et al., 2000; Farnsworth et al., 2002; McCallum, 2005; Sutherland et al., 2019). These models reduce biases in population density estimates because they focus on the inherent structure that exists both within populations (such as sex) and between populations that have some level of spatial or temporal independence (such as session). All analyses were done using the R software (R Core Team, 2019) using the package oSCR (Sutherland et al., 2019). Model selection was based on Akaike information criterion (AIC) following Arnold (2010). The tests were considered significant at $p < 0.05$.

Results and Discussion

Birds

In total, 1,813 birds were captured (includes recaptures), comprising 82 species in 29 families during 42,480 netting hours under closed canopy and in forest gap locations. Of these, 961 individual birds in 68 species were at closed canopy sites and 852 individuals in 64 species were caught at forest gap sites. The three most commonly captured families were the Leiothrichidae, Muscicapidae and Timaliidae. Insectivore was the group with the largest recapture count for analyzing individual data. The four most frequently caught insectivore species were the Grey-cheeked Fulvetta (*Alcippe fratercula*), Hill Blue Flycatcher (*Cyornis banyumas*), Grey-throated Babbler (*Stachyris nigriceps*) and Orange-headed Thrush (*Geokichla citrina*), and the most commonly captured species were the Grey-cheeked Fulvetta ($n = 325$), Hill Blue Flycatcher ($n = 234$) and Grey-throated Babbler ($n = 191$), as shown in Table 1. Seventeen species were captured only at closed canopy sites versus 15 at forest gap sites; 51 species occurred in both areas. Table 1 summarizes the captures and recaptures for the closed canopy and forest gap sites and the feeding guild designation of each species. Insectivore was the most abundant group (586 species caught in closed canopy, 696 species caught in forest gaps), followed by frugivore (86 in closed canopy, 105 in forest gaps), nectarivore (15 in closed canopy, 51 in forest gaps) and carnivore (1 in closed canopy)

Table 1 Species and number of understory birds captured and recaptured in closed canopy and forest gaps in Mae Sa-Kog Ma Biosphere Reserve, Northern Thailand

Feeding guild/Species	Number captured in closed canopy (number recaptured)						Number captured in forest gaps (number recaptured)					
	2014	2015	2016	2017	2018	2019	2014	2015	2016	2017	2018	2019
Frugivore												
Alophoixus pallidus	4	4	17 (4)	11 (5)	12 (8)	4 (1)	1	6 (1)	13 (2)	1 (3)	1 (7)	1 (4)
Chalcophaps indica	-	-	-	-	1	-	-	1	1	1	2	1
Erythrura prasina	-	-	-	-	-	-	1	1	-	-	-	-
Hemixos flavala	-	1	-	-	-	1	-	-	-	1	1	-
Ixos mcclellandii	1	4	8	7 (2)	4	2 (2)	8 (1)	3	7 (1)	6 (2)	1	9 (4)
Megalaima asiatica	-	-	-	-	1	-	-	2	-	2	1	-
Pycnonotus flavescens	-	-	-	-	-	-	-	-	-	-	1	-
Pycnonotus flaviventris	1	-	2	1	-	-	-	4	-	1	-	-
Insectivore												
Abroscopus superciliaris	-	-	-	-	-	-	-	-	-	1	5 (2)	-
Alcippe fratercula	14 (3)	12 (7)	49 (30)	28 (17)	24 (13)	17 (13)	8	37 (10)	29 (18)	58 (37)	3 (25)	19 (14)
Cacomantis sonneratii	-	-	-	-	1	-	-	-	-	-	-	-
Cissa chinensis	-	-	-	-	1	1	-	-	-	-	1 (1)	-
Clamator coromandus	-	-	1	-	-	-	-	-	-	-	-	-
Cochoa viridis	-	-	-	-	1	-	-	-	-	-	-	-
Copsychus malabaricus	-	2	1	3 (2)	5	8 (1)	-	3 (1)	1	-	4 (1)	4 (2)
Cuculus poliocephalus	-	1	-	-	-	-	-	-	-	-	-	-
Culicicapa ceylonensis	-	-	-	1	-	1 (1)	1	1	2	-	1 (1)	1 (1)
Cyornis banyumas	1	19 (3)	33 (8)	46 (14)	33 (10)	15 (6)	1	9 (4)	12 (5)	27 (6)	22 (6)	16 (4)
Cyornis rubeculoides	-	-	-	-	-	1	-	-	-	-	-	-
Dicrurus aeneus	-	1	-	-	-	-	-	-	-	-	-	1
Dicrurus paradiseus	-	-	-	-	-	-	-	-	-	-	-	1
Dicrurus remifer	-	-	-	3	-	1	-	1	1	-	1	1
Dryonastes chinensis	-	-	-	-	-	1	-	1	-	-	-	-
Enicurus leschenaulti	-	2	2 (1)	-	3 (1)	2 (1)	-	-	-	1 (1)	1 (1)	1 (1)
Erpornis zantholeuca	-	-	1	1	1	-	1	1	4	7 (3)	6	2
Eumyias thalassinus	-	-	-	1	-	-	-	-	-	-	-	-
Ficedula hyperythra	1	1	-	1	1	-	-	-	-	-	-	-
Garrulax chiesis	1	2 (1)	2 (1)	1	-	2	4	2 (2)	2	2	1	1
Garrulax monileger	2 (1)	-	-	2	-	-	-	-	-	-	-	-
Garrulax pectoralis	-	-	-	-	1	-	-	-	-	-	-	-
Garrulax strepitans	-	-	-	-	-	1 (1)	-	-	-	-	-	1 (1)
Geokichla citrina	-	3	7	12 (2)	5	7 (1)	-	4 (1)	3	5	2	1
Hydrornis cyaneus	-	-	-	3	2	-	-	-	-	1	1	1 (1)
Hypothymis azurea	-	4	2 (2)	3 (2)	2	1 (1)	2	1	3	4 (1)	4 (2)	1 (1)
Lanius tephronotus	-	-	-	-	-	-	-	-	-	-	-	1
Larvivora cyane	-	-	2	-	-	3	-	-	-	-	1	1
Macronus gularis	-	-	-	-	3 (1)	-	-	2	2 (2)	6 (2)	3 (1)	1 (1)
Monticola rufiventris	-	1	-	-	-	-	-	-	-	-	-	-
Muscicapa ferruginea	1	-	-	-	-	-	-	-	-	1	-	-
Myiomela leucura	1	1	2	4 (1)	5	3 (2)	-	-	-	-	1 (1)	-
Myophonus caeruleus	-	-	1	1	-	1	-	-	-	-	1 (1)	-
Napothera epilepidota	-	-	3 (1)	1	5	1 (1)	-	-	-	-	-	-
Niltava sundara	1	2	4 (2)	5 (1)	7 (3)	2 (1)	-	-	1	1	2 (1)	1
Pellorneum ruficeps	-	5 (2)	2 (1)	6 (3)	4 (2)	1	-	1	-	-	-	-
Pellorneum tickelli	-	7 (1)	12 (2)	9 (2)	8 (3)	4 (4)	-	-	-	2	2 (2)	2

Table 1 (Continued) Species and number of understory birds captured and recaptured in closed canopy and forest gaps in Mae Sa-Kog Ma Biosphere Reserve, Northern Thailand

Feeding guild/Species	Number captured in closed canopy (number recaptured)						Number captured in forest gaps (number recaptured)					
	2014	2015	2016	2017	2018	2019	2014	2015	2016	2017	2018	2019
Phylloscopus armandii	-	-	-	-	2 (1)	-	-	-	-	-	-	-
Phylloscopus davisoni	-	1	-	1	3 (3)	1 (1)	-	1	1	1	3 (2)	1
Phylloscopus inornatus	-	-	-	-	-	-	-	1	-	-	-	-
Phylloscopus reguloides	-	2	4	7	3 (1)	2	4	2	13	13 (5)	1 (1)	4 (2)
Phylloscopus ricketti	-	-	2	2	-	3	2	1	1	11 (2)	7 (2)	1
Phylloscopus tenellipes	-	-	-	1	-	1	-	-	-	-	-	-
Phylloscopus yunnanensis	-	-	-	-	-	-	-	-	-	-	1	-
Picumnus innominatus	-	2	1	4 (2)	4 (1)	1	-	1	8 (3)	4 (2)	5 (2)	-
Picus guerini	-	-	-	-	-	-	-	-	-	2	-	-
Pomatorhinus schisticeps	-	-	2	1	-	-	-	-	-	-	1	-
Psarisomus dalhousiae	-	-	-	-	-	-	-	-	-	-	1	-
Pteruthius flaviscapis	-	-	2	-	-	-	-	-	-	-	1	-
Pteruthius intermedius	-	-	-	2 (1)	3 (1)	1	-	2	4 (1)	2	1 (1)	2 (2)
Rhipidura albicollis	1	1	1	1	-	-	-	3	3 (1)	1	1	-
sasia ochraceu	1	1 (1)	-	1	3 (1)	2 (1)	-	1	1	-	-	1 (1)
Seicercus omeiensis	1	5 (1)	6	11 (2)	4 (1)	3 (1)	4	3	11 (2)	9 (4)	1 (1)	3 (1)
Seicercus valentini	2	2 (1)	12 (4)	12 (3)	15 (5)	8 (2)	1	2	9 (5)	6 (2)	13 (9)	4 (2)
Serilophus lunatus	-	8	4	2 (1)	3	7	-	-	-	1	6	9 (2)
Sitta frontalis	-	-	-	1	-	-	-	2	1	4 (1)	1	1 (1)
Stachyris nigriceps	18 (6)	2 (10)	22 (12)	26 (16)	31 (18)	21 (14)	1	4 (2)	8 (6)	19 (9)	11 (3)	1 (6)
Staphida castaniceps	-	-	-	-	-	-	-	1	-	-	-	-
Terpsiphone paradisi	-	-	1	-	1	-	-	-	4	-	-	1
Tropicoperdix chloropus	-	-	-	-	1	-	-	-	-	-	-	-
Turdus dissimilis	-	-	-	-	2	1	-	-	-	-	-	-
Turdus obscurus	-	-	2	-	-	-	-	-	-	-	-	-
Urosphena squameiceps	-	1	2 (1)	4 (1)	-	-	-	-	-	-	-	-
Zoothera dauma	-	-	-	-	-	2	-	-	-	-	-	1
Zoothera marginata	-	-	-	1	-	-	-	-	-	-	-	-
Zosterops Erythropleuru	-	-	-	-	-	-	-	-	-	4	3	5
Zosterops palpebrosus	-	-	1	-	-	-	-	-	1	-	3	2
Nectavivore												
Aethopyga saturata	1	-	1	1 (1)	2 (2)	-	-	1	7	3 (1)	4 (2)	2 (1)
Arachnothera longirostra	1	1	2 (1)	-	-	1	1	3 (2)	3 (1)	1 (2)	1 (1)	4 (3)
Arachnothera magna	1	-	2	2	-	-	-	4	3	3	1	5
Chalcoparia singalensis	-	-	-	-	-	-	-	-	-	-	1	-
Chloropsis hardwickii	-	-	-	-	-	-	-	2	-	-	-	-
Dicaeum ignipectus	-	-	-	-	-	-	-	-	-	2	-	-
Carnivore												
Glaucidium brodiei	-	-	1	-	-	-	-	-	-	-	-	-

Of the birds captured, 602 individual birds of 38 species were recaptured, consisting of 317 individuals (52.65%) of 32 species at forest gap sites and 285 individuals (47.34%) in 36 species at closed canopy sites. While more individuals were recaptured at closed canopy sites, more species were caught at forest gaps sites. The most frequently recaptured individual was a Hill Blue Flycatcher that was recaptured nine and six times at closed canopy and forest gap sites, respectively. A Grey-cheeked Fulvetta was recaptured 3 and 10 times at closed canopy and forest gap sites, respectively and a Grey-throated Babbler was recaptured nine and two times at closed canopy and forest gap sites, respectively (Fig. 2).

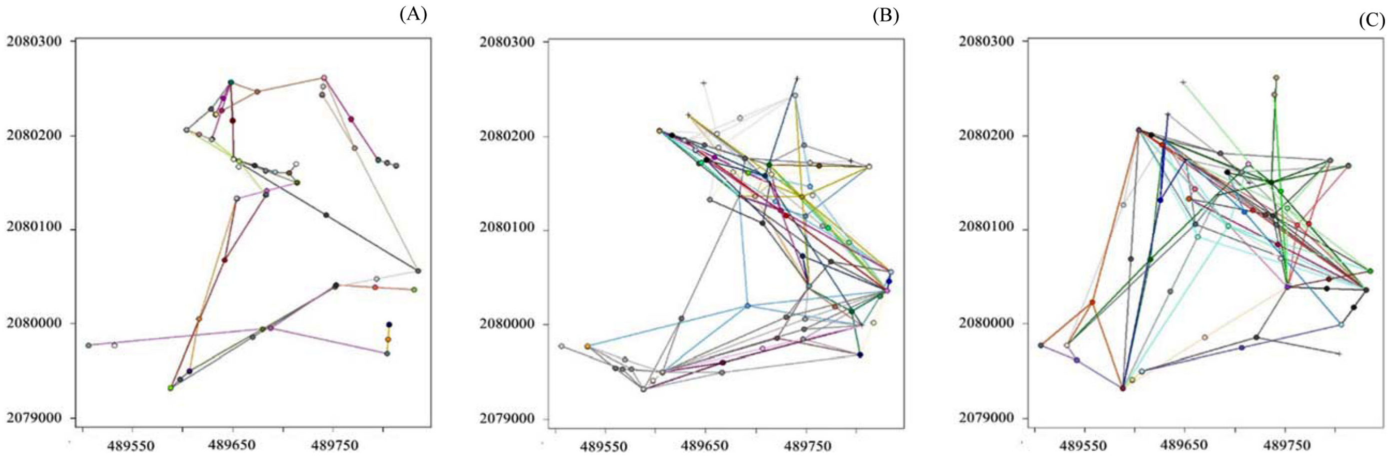

Fig. 2 Spatial models of movement and detection probability for: (A) Hill Blue Flycatcher; (B) Grey-cheeked Fulvetta; (C) Grey-throated Babbler in closed canopy and forest gaps, where each filled circle represents spatial average of all detections of an individual and lines join average locations to traps in which individuals were captured, each unique color (circles and lines) indicate a unique individual, Crosses (+) are trap locations and circles without lines are individuals that were detected at only a single location (gaps locations recorded using UTM 84 zone 47N coordinate system)

In other reports, insectivorous birds accounted for the largest proportion of understory birds (Round et al., 2011; Shermila and Wikramasinghe, 2013; Siri et al., 2019). The current study identified consistent significant differences in the study area in the responses of guilds. Although the guilds were coarsely classified, the species feeding guild may predict vulnerability to disruption of insects. The gap variables of canopy openness that most influenced bird community composition were related to sunlight exposure (Banks-Leite and Cintra, 2008). As noted by Uhl et al. (1988) and Whitmore (1989), the fruiting success of plants is also influenced by gap characteristics, with the density of fruiting plants tending to increase with gap size (Levey, 1988). Tree fall gaps may also harbor a greater density of insects than mature forest (Malmborg and Willson, 1988; Richards and Coley, 2007). Consequently, many birds may be attracted to gaps in response to the increased food availability (Blake and Hoppes, 1986) Therefore, frugivorous and nectarivorous birds were the guilds most affected by canopy closure following gaps reverting to natural forest with plant succession.

Spatial models of movement and detection probability of the feeding guilds in the closed canopy and forest gaps are provided in Fig. 3.

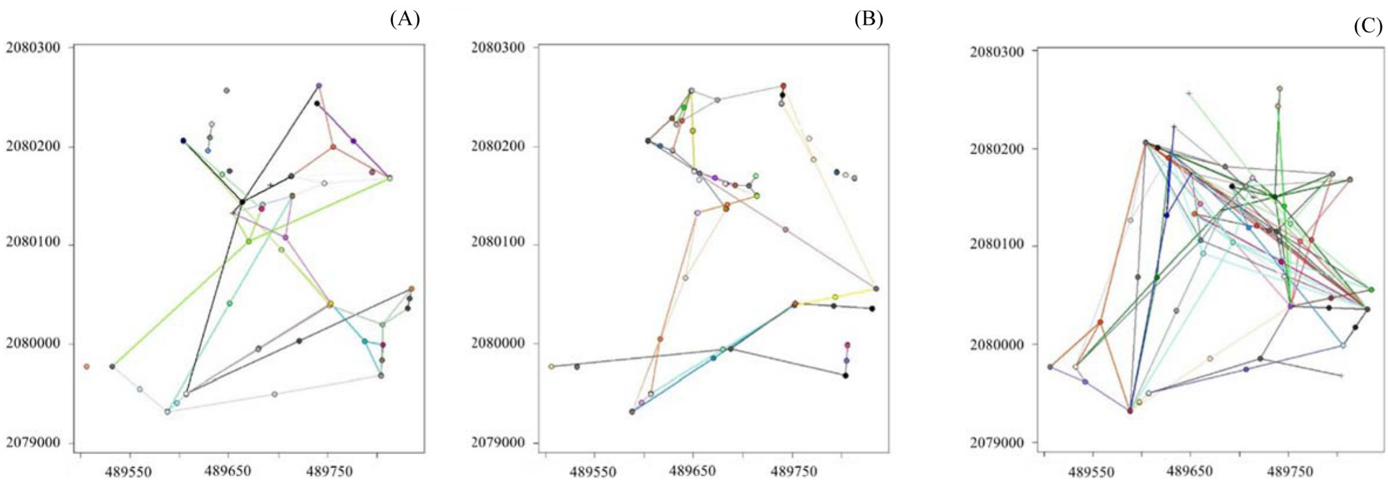

Fig. 3 Spatial model of movement and detection probability for one session feeding guilds: (A) frugivorous; (B) insectivorous; (C) nectarivorous in closed canopy and forest gaps, where each filled circle represents spatial average of all detections of an individual and lines join average locations to traps in which individuals were captured, each unique color (circles and lines) is a unique individual, crosses (+) are trap locations and circles without lines are individuals that were detected at only a single location (gaps locations recorded using UTM 84 zone 47N coordinate system)

Detection probability

Based on 60 monthly data points, the probability of detecting bird species was grouped into feeding guilds. However, the differences in the of detection probabilities were not significant (Table 2). Based on the program oSCR, the best model (lowest AIC value) was more supportive of a constant density across sites than between-site variability, with cumulative model weights of 0.184, 3.67, 0.356, and 1.68, respectively (Table 3). From an overview of all captures, the most fitting model was for detection probability by gap, gap interaction with month, and movement; for frugivorous detection probability it was by month, month interaction with a gap, and movement; for insectivorous detection probability it was by the gap, month, and movement; and for nectarivorous was by gap and movement, as shown in Table 3. Based on the AIC values, the most influential factors affecting the population were occasion and gap age between closed canopy and forest gaps sites. Out of 1,813 birds, the detection probabilities of bird species were grouped into feeding guilds.

All first-time captures (Fig. 4A) and frugivores (Fig. 4B) had higher habitat utilization in closed canopy than in forest gaps. For the closed canopy sites, the habitat utilization in the following month was still higher than that of the forest gaps sites, and in the forest gaps it gradually increased. Frugivorous birds foraged more frequently in gaps relative to the forest interior, presumably because the gaps provided excellent fleshy fruit as a food resource for frugivores, especially small-sized fruit (Rueangket et al., 2021) and could accommodate an increasing population until reaching carrying capacity. The bird population in forest gaps initially increased over time and then fell, consistent with Khamcha and Gale (2012) and Ponpithuk et al. (2020). Compared to the closed canopy undisturbed understory environment, forest gaps can also experience an increased density of insects due to changes in microclimatic conditions and the density of regeneration growth (Richards and Coley, 2007). It was possible that birds were attracted to the gaps by the high luminosity levels and foliage density (Champlin et al., 2009), perhaps inducing a greater abundance of insects. Some studies have revealed that the fruits in these areas are brighter and thus may be more easily noticed by birds and therefore more readily eaten (Willson et al., 1982). This was consistent with Rosely et al. (2007), who detected significantly more birds in gaps than in the forest interior. Open conditions provided better foraging for various species, making this better habitat for a wide range of species (Raman et al., 1998; Chettri et al., 2001). In the current study, the pooled abundance increased with canopy openness.

Table 2 Regression coefficients of top model describing variability in density (D) baseline detection (p_0) and space use (σ) of feeding guild classification as function of site, session and time

Model	Estimate	SE	P(>|z|)
(A) All capture			
p0.(Intercept)	-5.678	0.059	0
t.beta.gap	-0.223	0.079	0.005
t.beta.gap:month	0.004	0.002	0.076
sig.(Intercept)	4.489	0.034	0
d0.(Intercept)	1.996	0.053	0
(B) Frugivore			
p0.(Intercept)	-5.795	0.07	0
t.beta.month	0.003	0.002	0.039
t.beta.month:gap	-0.002	0.001	0.107
sig.(Intercept)	4.489	0.034	0
d0.(Intercept)	1.996	0.053	0
(C) Insectivore			
p0.(Intercept)	-5.741	0.073	0
t.beta.gap	-0.114	0.047	0.016
t.beta.month	0.002	0.001	0.132
sig.(Intercept)	4.489	0.034	0
d0.(Intercept)	1.996	0.053	0
(D) Nectarivore			
p0.(Intercept)	-6.277	0.398	0
t.beta.gap	1.228	0.295	0
sig.(Intercept)	4.382	0.179	0
d0.(Intercept)	-0.875	0.276	0.002

In the insectivore group (Fig. 4C), the initial detection probability was higher in the closed canopy than for the forest gaps sites, and both initially increased. These findings were similar to those from studies conducted in temperate regions where species numbers and abundance increased in managed gaps compared with those in continuous forest (Forsman et al., 2010). More nectarivores (Fig. 4D) were found in forest gaps than at the closed canopy sites, but the detection probability was constant in both areas. Many forest gaps supported populations of *Phlogacanthus curviflorus* (Wall.), which is a source of nectar (Siri et al., 2019). Nectarivore density did not change significantly following disturbance. This differed from Levey (1988) and Wunderle et al. (2005), who found that tropical frugivorous and nectarivorous birds attained higher abundance and diversity in gaps, likely reflecting concurrent increases in resource availability, such as flowering and fruiting plant species. Bird species feed on a wide variety of food items and the responses of species to habitat disturbances differ according to the feeding guild (Pearman, 2002; Gray et al., 2007). For example, insectivores might increase, decrease or show no apparent change in diversity following forest disturbance (Thiollay, 1992; Andrade and Rubio-Torgler 1994; Waltert et al., 2004).

Table 3 Variability in density (*D*) and baseline detection (*p0*) of feeding guilds as function of gap, occasion and session for bird population in permanent lower montane forest plot, using the oSCR program and best model based on lowest Akaike information criterion (AIC) value for all captures and observations summed as closed canopy and forest gaps in Mae Sa-Kog Ma Biosphere Reserve in Doi Suthep-Pui National Park, Northern Thailand

Guild	Model (*p0*)	LogL	K	AIC	dAIC	Weight	CumWt
All capture	[1]D(~1) p(~gap + gap:month) sig(~1)	6086	5	12182	0	0.347	0.35
	[2]D(~1) p(~gap + month) sig(~1)	6086	5	12183	0.87	0.224	0.57
	[3]D(~1) p(~gap) sig(~1)	6088	4	12183	1.14	0.197	0.77
	[4]D(~1) p(~gap + month + gap:month) sig(~1)	6086	6	12184	1.84	0.138	0.91
	[5]D(~1) p(~month + month:gap) sig(~1)	6088	5	12186	4.07	0.045	0.95
	[6]D(~1) p(~month) sig(~1)	6089	4	12187	4.66	0.034	0.99
	[7]D(~1) p(~gap:month) sig(~1)	6090	4	12188	6.28	0.015	1
Frugivore	[5]D(~1) p(~month + month:gap) sig(~1)	831	5	1671	0	0.323	0.32
	[6]D(~1) p(~month) sig(~1)	832	4	1672	0.53	0.247	0.57
	[2]D(~1) p(~gap + month) sig(~1)	831	5	1672	0.73	0.224	0.79
	[4]D(~1) p(~gap + month + gap:month) sig(~1)	831	6	1673	2.0	0.119	0.91
	[3]D(~1) p(~gap) sig(~1)	834	4	1676	4.14	0.041	0.95
	[1]D(~1) p(~gap + gap:month) sig(~1)	833	5	1676	4.81	0.029	0.98
	[7]D(~1) p(~gap:month) sig(~1)	835	4	1677	5.86	0.017	1
Insectivore	[2]D(~1) p(~gap + month) sig(~1)	5506	5	11022	0	0.36301	0.36
	[1]D(~1) p(~gap + gap:month) sig(~1)	5506	5	11022	0.16	0.3354	0.7
	[4]D(~1) p(~gap + month + gap:month) sig(~1)	5506	6	11023	1.08	0.21136	0.91
	[3]D(~1) p(~gap) sig(~1)	5509	4	11025	3.13	0.07581	0.99
	[5]D(~1) p(~month + month:gap) sig(~1)	5509	5	11029	6.54	0.01382	1
	[6]D(~1) p(~month) sig(~1)	5514	4	11036	13.44	0.00044	1
	[7]D(~1) p(~gap:month) sig(~1)	5515	4	11038	15.51	0.00016	1
Nectarivore	[3]D(~1) p(~gap) sig(~1)	313	4	634	0	3.40E-01	0.34
	[5]D(~1) p(~month + month:gap) sig(~1)	312	5	634	0.86	2.20E-01	0.57
	[2]D(~1) p(~gap + month) sig(~1)	313	5	635	1.61	1.50E-01	0.72
	[4]D(~1) p(~gap + month + gap:month) sig(~1)	312	6	635	1.7	1.50E-01	0.87
	[1]D(~1) p(~gap + gap:month) sig(~1)	313	5	636	1.99	1.30E-01	1
	[7]D(~1) p(~gap:month) sig(~1)	317	4	643	9.33	3.20E-03	1
	[6]D(~1) p(~month) sig(~1)	323	4	654	20.35	1.30E-05	1

K = Model parameters; ΔAIC = The difference in AIC score between the best model and the model being compared CumWt = cumulative weight.

m1 <- D(~1) p(~gap + gap:month) sig(~1) = Detection probability by gap, gap interaction with month, and movement.

m2 <- D(~1) p(~gap + month) sig(~1) = Detection probability by gap, month and movement.

m3 <- D(~1) p(~gap) sig(~1) = Detection probability by gap and movement.

m4 <- D(~1) p(~gap + month + gap:month) sig(~1) = Detection probability by gap, month, gap interaction with month, and movement.

m5 <- D(~1) p(~month + month:gap) sig(~1) = Detection probability by month, month interaction with gap, and movement.

m6 <- D(~1) p(~month) sig(~1) = Detection probability by month and movement.

m7 <- D(~1) p(~gap:month) sig(~1)= Detection probability by interaction with month and movement.

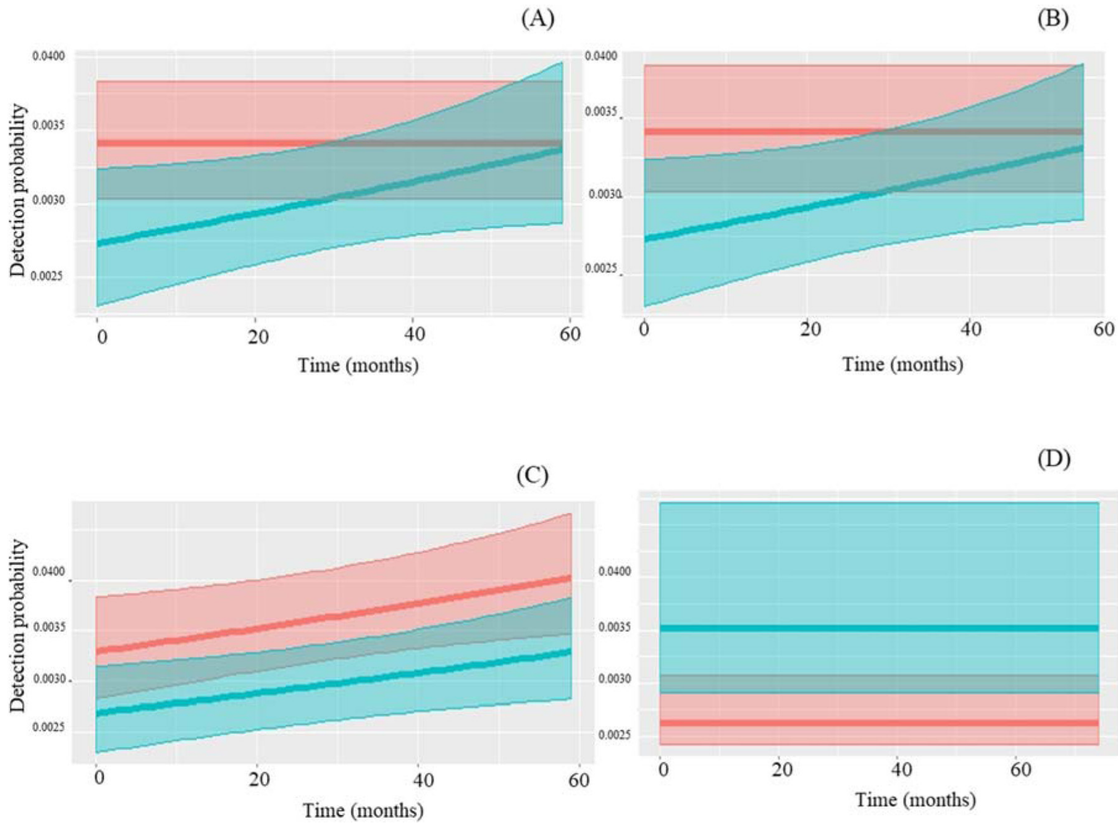

Fig. 4 Monthly detection probability of feeding guild birds in closed canopy and forest gaps: (A) all captures; (B) frugivores; (C) insectivores; (D) nectarivores

Fig. 5 shows the four insectivorous bird species captured most frequently. Comparing the detection probability with gap age over time, the Hill Blue Flycatcher (Fig. 5A) and Grey-throated Babbler (Fig. 5B) were similar. The detection probability was initially higher in the closed canopy than at the forest gaps sites, but this increased gradually in the forest gaps. As gap age increased, the detection probabilities of some bird species declined, especially for the Grey-cheeked Fulvetta (Fig. 5C) and Orange-headed Thrush (Fig. 5D). The detection probability in FGs was low. In general, insectivorous birds were disproportionately sensitive to land-use intensification and habitat loss. These species feed primarily on the ground in dense forest (Stouffer, 2007; Watson, 2015).

The current results suggested that forest gaps function as keystone habitats for some birds as noted in other studies (Levey, 1990; Siri et al., 2019). At the species-group level, the presence of a gap had negligible effects on some bird population densities. Only ground foragers showed a slow decrease in density in response to gaps. Regardless, understory disturbance was needed to maintain diversity in these forests and the forest gaps can provide essential resources for many woodland bird species. Li et al. (2020) highlighted the importance of remnant microhabitats in fragmented forests for sustaining forest ecology and optimal management. With the contribution of microhabitats used by birds, there is reason to believe that birds can recognize and select tree-fall gaps as a distinct microhabitat in which to forage. Birds may well be attracted to gaps due to the abundance of food resources (insects) and perhaps nesting material. The abundance of arthropod foods, nesting material, microsites for nesting and vegetative structures could be primary factors that attract breeding birds to forest gaps. Habitat heterogeneity was a significant environmental determinant of species richness only for nectarivorous birds (Fig. 4D) and the Grey-throated Babbler (Fig. 5B), which preferred forest gaps and shade-tolerant canopy, respectively. The current study illustrated the importance of forest gaps in supporting frugivorous and insectivorous birds, while nectarivore populations remained stable. Forest gaps may function as keystone habitats for birds to sustain frugivores and nectarivores during periods of fruit scarcity in the forest. In addition, canopy openings in continuous forest may maintain high avian diversity in tropical forests.

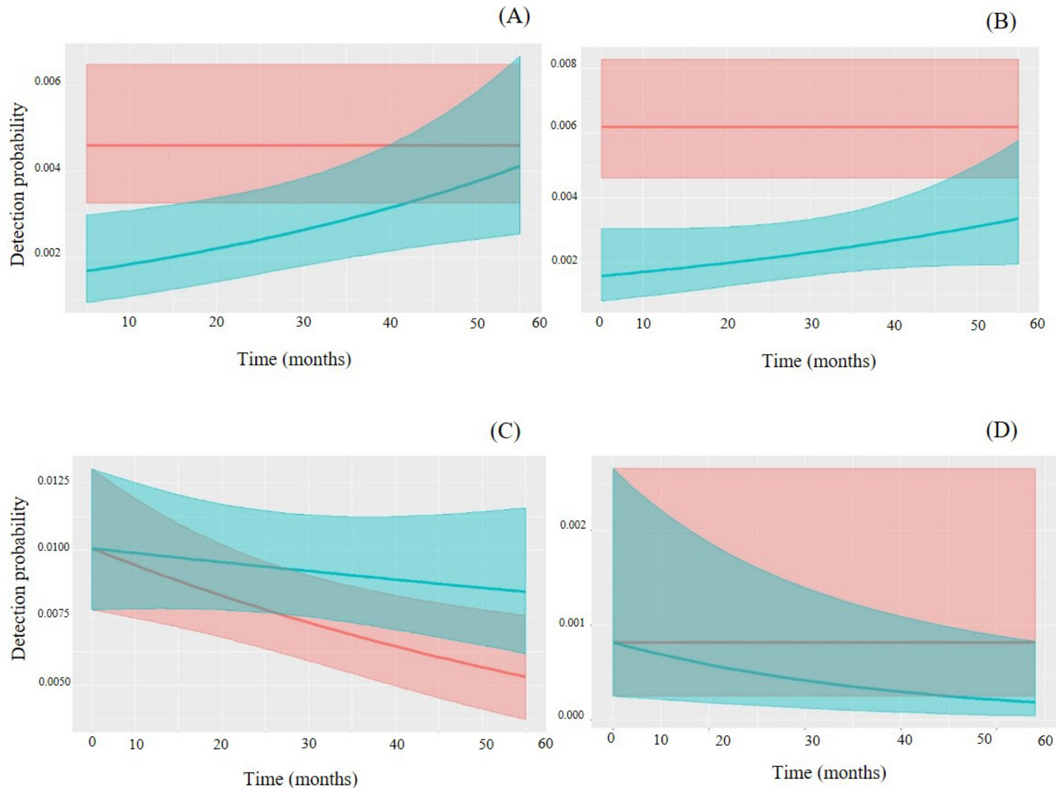

Fig. 5 Monthly detection probability of selected insectivores in closed canopy and forest gaps: (A) Hill Blue Flycatcher; (B) Grey- throated Babbler; (C) Grey-cheeked Fulvetta; (D) Orange-headed Thrush

Conflict of Interest

The authors declare that there are no conflicts of interest.

Acknowledgments

The Department of National Parks and Wildlife and Plant Conservation, Mae Sa-Kog Ma Biosphere Reserve, Doi Suthep-Pui National Park, and Doi Chiang Dao Wildlife Reserve Station, Chiang Mai Province gave permission to conduct this study. Fieldwork assistance was provided in particular by other students at the Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok, Thailand.

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