DISSERTATION

# AVIAN CONSERVATION AND ECOLOGY IN NORTHERN VIETNAM

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY THINH TIEN VU ENTITLED AVIAN CONSERVATION AND ECOLOGY IN NORTHERN VIETNAM BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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### ABSTRACT OF DISSERTATION

#### IMPROVING AVIAN CONSERVATION IN NORTHERN VIETNAM

Vietnam is a tropical country rich in biodiversity. For example, ten percent of the world's mammals, birds, and fishes are found in Vietnam which accounts for only 0.3% of the world's land mass. Vietnam is not only rich in species but also rich in species endemism. However, biodiversity in Vietnam has been declining at a rapid rate due primarily to habitat degradation, especially in natural forests. How best to conserve the avian biodiversity in Vietnam is a contemporary issue of concern and my dissertation was aimed at several issues focused on avian conservation in Vietnam.

Recently, overall forest cover in Vietnam has increased, but most of the increase has been attributed to plantations of non-native trees. The avian conservation potential of these plantations remains unknown. In Chapter 1, I examined the conservation potential of pine plantations by comparing bird species supported in pine plantations to other natural vegetation types including secondary growth forests and mature forests in Tam Dao National Park, northern Vietnam. I estimated total species richness and number of forest specialist species to be highest in mature forest (143.88; 95% CI = 95.23, 192.54, and 88.08; 95% CI = 46.94, 129.22 respectively), lower in secondary growth (111.99 (95% CI = 75.47, 148.51 and 57.51; 95% CI = 17.51, 97.51 respectively), and lowest in pine plantation (83.24; 95% CI = 53.75, 112.74 and 49.45; 95% CI = 1.84, 97.06

respectively). The number of forest generalist species was estimated to be similar between mature forest and secondary growth forest (103.28; 95% CI = 17.24, 189.31 and 100.41; 95% CI = 42.36, 158.47, respectively) and least in pine plantation (56.57; 95% CI = 31.28, 81.85). I suggest that natural forest types should receive priority for conservation in Vietnam and pine plantations should be managed to provide additional structure in hopes of increasing avian species richness.

In addition to the loss of natural forests, forest fragmentation also contributes to the degradation of natural habitat for wildlife species. Linear gaps such as roads that are being imposed increasingly onto forest landscapes constitute a critical wildlife conservation concern in Vietnam. In Chapter 2, I used playbacks of territorial calls to investigate the effects of linear gaps (e.g., by roads and powerlines) on bird movement. Specifically, I compared bird movement over a paved road (6-8m wide) and within forest interior plots in Cuc Phuong National Park, northern Vietnam in summer 2007. I focused on two groups of species in the Sylviidae family: a mid-canopy foraging group and a ground-feeding group. The probabilities of approaching the playback were higher for mid-canopy species than for the ground species. The probabilities of approaching the playback for mid-canopy species at the road sites (0.92; 95% CI = 0.84, 0.97 for Striped)Tit Babbler and 0.88, 95% CI = 0.78, 0.94 for Rufous-throated Babbler) were similar to those in forest interior (0.96; 95% CI = 0.88, 0.98 for Striped Tit Babbler and 0.93; 95% CI = 0.84, 0.97 for Rufous-throated Fulvetta). The probabilities of approaching the playback for ground species at the road site (0.77; 95% CI = 0.66, 0.86 for Puff-throated)Babbler and 0.69; 95% CI = 0.57, 0.78 for Buff-breasted Babbler) were lower than those in the forest interior (0.85; 95% CI = 0.73, 0.92 for Puff-throated Babbler and 0.82; 95%

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CI = 0.72, 0.89 for Buff-breasted Babbler). The response delay time of the mid-canopy group was less than the response delay time of the ground species. The response delay times for all species at the road sites (2.39 minutes; 95% CI = 1.85, 2.92 for Striped Tit Babbler, 2.50; 95% CI = 1.96, 3.04 for Rufous-throated Babbler, 3.27 minutes; 95% CI = 2.75, 3.79 for Puff-throated Babbler, and 3.23 minutes; 95% CI = 2.72, 3.75 for Buff-breasted Babbler) were slightly less than those in forest interior (2.11; 95% CI = 1.69, 2.52 for Striped Tit Babbler, 2.22; 95% CI = 1.74, 2.70 for Rufous-throated Fulvetta, 3.10; 95% CI = 2.60, 3.54 for Puff-throated Babbler, and 3.03 minutes; 95% CI = 2.60, 3.47 for Buff-breasted Babbler). The road seems to moderately affect the ability for ground-feeding species of bird to cross gaps and not to affect species that live mostly in the mid-canopy and high canopy. These roads, especially in the natural reserves, should be designed to be as narrow as possible, and to keep the forest canopy over the gaps as closed as possible. In the areas where ground birds are of interest or endangered, road construction should be avoided.

Balancing economic activities, such as logging, with conservation programs will play an important role in conserving the rich biodiversity in these regions and the effects of logging on biodiversity needs to be understood more thoroughly. In Chapter 3, I modeled the recovery of avian communities following a variety of potential logging schemes that varied by the logging interval (1-100 years in steps of five years) and the wood volume left after harvesting (0-100 % in steps of five percents). The recovery rate of forest generalists is very high during the first 15 years of succession and then becomes asymptotic. The recovery rate of forest specialists remains high until about 50 years of succession. After 50 years, the recovery rate is lower, and fewer bird species colonized in future years. Logging schemes with either logging cycle > 15 years or wood volume left after harvesting > 30% resulted in 70% of the regional forest bird species pool being conserved. To conserve 80% of the species pool, logging schemes with either cycle length > 40 years or wood volume left after harvest > 55% should be implemented. My simulations provide a prediction of how avian communities could be affected under different logging schemes and can provide guidance to management agencies in developing tropical forested countries.

Wildlife diseases are gaining increasing attention given concerns over the role humans may play in emerging wildlife diseases and the impacts pathogens may have on vulnerable wildlife populations. The avian blood parasites, or haemosporidia, make up one such group of parasites linked to critical conservation concerns. Given these conservation concerns and a paucity of information on avian blood parasites in birds in Vietnam, Chapter 4 was aimed at characterizing the sample prevalence of avian blood parasites that cause avian malaria and investigating the ecological factors affecting prevalence in free-ranging wild land birds. I focused on two genera of blood parasites including *Plasmodium spp.* and *Haemoproteus spp.* that cause malaria in birds. Samples were collected in Cuc Phuong and Tam Dao National Parks, northern Vietnam in summer 2007 and 2008. The overall prevalence of avian malaria (AM) in sample birds was 45.85%. Infections were detected in the majority of bird species sampled. The sample prevalence did not differ by sampling regions and habitats. However, higher parasite prevalence was observed in flocking species compared to solitary species and higher parasite prevalence was observed in adult birds compared to juvenile birds. This is the first documented occurrence of AM in Vietnam.

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Avian influenza (AI) viruses are currently considered one of the most important bird-associated groups of zoonotic pathogens. However, little information is available about the occurrence of AI viruses in land birds, especially in Southeast Asia including Vietnam, an area that is experiencing a relatively high incidence of outbreaks in humans and domestic poultry. To begin to fill this information gap, I focused on surveillance for the presence of AI virus nucleic acids and antibodies for AI viruses in free-ranging wild land birds in northern Vietnam in Chapter 5. In 2007, serum samples were collected from 197 birds. Serum samples from four birds were antibody positive for the H5 subtype of AI. In 2008, tracheal and cloacal swab samples were collected from 193 birds. Using the rRT-PCR test (without virus isolation), nine tracheal swab samples and one cloacal swab sample collected from 10 Japanese White-eyes (*Zosterops japonicus*) were positive for the influenza A virus M gene. Additionally, tracheal swab samples collected from other two Puff-throated Bulbuls (Alophoixus pallidus) tested positive. Following virus isolation, one tracheal swab sample collected from a White-tailed Robin (Cinclidium leucurum) and one tracheal swab sample collected from a Striped Tit Babbler (*Macronous gularis*) were positive for the viral M gene by rRT-PCR. Using both methods, 12 samples were positive for AI virus RNA and two were positive for viable AI virus, producing a sample prevalence of 7.25%. Tracheal swab samples make up 92.86% of positive sample and cloacal swab samples make up only 7.14% of positive samples, using both tests. Almost all positive samples were from birds that forage in flocks. Japanese White-eyes had an unusually high prevalence of 14.93%. This result suggests that attention should be given to land birds in AI surveillance and monitoring programs. Among land birds, special attention should be given to the social, flocking

species due to their higher AI prevalence compared to other groups. In particular, Japanese White-eyes may be an effective focal species in AI virus surveillance or monitoring programs in Southeast Asia. Both types of swab samples, tracheal (or oropharyngeal) and cloacal, should be collected and processed if both HPAI and LPAI virus detection is of interest. Lastly, more studies should focus on the link between the incidence of outbreaks of HPAI in domestic poultry and the presence of HPAI viruses in land birds close to the outbreak sites.

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#### INTRODUCTION

### AVIAN CONSERVATION AND ECOLOGY IN NORTHERN VIETNAM

Vietnam is a tropical country rich in biodiversity. For example ten percent of the world's mammals, birds, and fishes are found in Vietnam. Vietnam is not only rich in species but also rich in species endemism. However, biodiversity in Vietnam has been declining at a rapid rate due primarily to habitat degradation, especially in natural forests (Nhat 2001). This is the result of economic development that utilizes and affects natural resources. How best to conserve the wildlife species in general and avian biodiversity in particular in Vietnam is a contemporary issue of concern and my dissertation was aimed at several issues focused on avian conservation and ecology in Vietnam. The dissertation includes five chapters.

The extreme reduction of natural forest cover worldwide is a current cause of concern (Collar et al. 1994, Sodhi et al. 2008). Declines in natural forest cover have been observed in Southeast Asia, including Vietnam, leading to the local extinction of many bird populations (Sodhi and Brook 2006). Recently, overall forest cover in Vietnam has increased, but most of the increase has been attributed to plantations of non-native trees, and natural forests are still being reduced and replaced by other land uses (Nhat 2001). The conservation value of these plantations for birds is unknown although few natural forest bird species are assumed to persist in other land uses (Hughes et al. 2002). Recent

evidence suggests that some land uses, such as tree plantations, can have great potential for forest bird species conservation, especially with management practices that diversify the forest vegetation and composition (Beukema et al. 2007, Reitsma et al. 2001).

Managing industrial forests in Vietnam for the dual purposes of wood production and conservation is of wide national interest in Vietnam. The recently proposed plan "Five Million Hectares of Forest" (Vietnam Government 1998) would increase the forest cover nationwide in Vietnam from 33% to 45% by planting non-native tree plantations. Overall benefits of this plan will be enhanced if conservation values can be incorporated into economic concerns. My objective in the first Chapter is to examine the avian conservation potential of pine plantations compared to other natural vegetation types including secondary growth forests and mature forests.

In addition to the loss of natural forest, forest fragmentation also contributed to the degradation of the natural habitat for wildlife species. Linear gaps such as roads that are being imposed into the forest landscapes raised critical concern of wildlife conservation in Vietnam. Roads have been shown to have adverse effects on wildlife in general, and birds in particular, in forested landscapes (Forman and Alexander 1998, Laurance et al. 2004). Roads can cause increased forest fragmentation, changes in plant composition, increased noise, and higher levels of exotic invasions by plant and wildlife species (Reijnen et al. 1995). These effects can lead to changes in bird community composition and population density of some species (Reijnen et al. 1995). Some species may be attracted to habitats near roads because of heterogeneous vegetation, but ultimately animals inhabiting these environments have lower survival and/or reproduction such that roads may cause such habitats to become ecological traps

(Schlaepfer et al. 2002), especially if animals die crossing roads (Forman and Alexander 1998, Mech 1989, Savidge et al. 1992).

Few studies have been conducted to demonstrate whether birds perceive roads as gaps and how bird movement is affected by such narrow linear gaps (Develey and Stouffer 2001, Laurance et al. 2004). No such studies have been conducted in tropical Southeast Asia. Understanding gap crossing ability in birds in Southeast Asia is important because this region supports a large area of tropical forest rich in bird species, has been identified as a conservation area of concern, especially for birds (Sodhi and Brook 2006), and is experiencing a high degree of economic development. This economic development leads to increased road and power line construction as well as an increased need for protecting wildlife in these areas. How such roads and power line corridors affect bird movement has not been considered by wildlife managers in this part of the world and this information will be useful to land planners in the face of rapid urbanization. In the second Chapter I examined whether forest birds in Southeast Asia are inhibited from crossing roads by using a territorial call playback. Specifically, I compared bird movement over a paved road (6-8m wide) within forest interior plots.

Most of the tropical forests in Asia are located in developing countries. These countries heavily utilize their natural resources, such as tropical forests, for development and setting aside all natural forests for preservation purposes is unrealistic. Therefore, balancing economic activities, such as logging, with conservation programs will play an important role in conserving the rich biodiversity in these regions. Bird communities are strongly influenced by habitat change (Terborgh et al. 1990, Wiens 1992), and are sensitive to disturbances. However, few studies have focused on the impacts of logging

on bird communities in the tropical forests, especially in Asia (Barlow et al. 2006, Dunn 2004, Holbech 2005, Lambert 1992, Mason 1996). These empirical studies have been limited to short term effects of a few logging schemes and have not revealed the long term recovery of avian communities after forest disturbance. Therefore in the third Chapter I simulated the effect of different logging schemes on tropical forest biodiversity, focusing on birds and I provide recommendations concerning logging cycles and the amount of wood volume that should be left after logging events.

Wildlife diseases are gaining increasing attention given concerns over the role humans may play in emerging wildlife diseases and the impacts pathogens may have on vulnerable wildlife populations (Daszak et al. 2004). To date, disease has led to the extinction of at least 31 animal species, of which 18 are avian species (Smith et al. 2006). In addition, the IUCN Red List includes 223 critically endangered animal species with disease as a 'contributing factor' (Smith et al. 2006).

The avian blood parasites, or haemosporidia, make up one such group of parasites linked to critical conservation concerns. Avian blood parasites, including those that cause avian malaria, have been implicated in the decline or loss of many bird populations including extinctions of 13 Hawaiian endemic forest bird species (Atkinson et al. 2000, Smith et al. 2006, Van Riper et al. 1986). Laird (1998) documented the presence of *Plasmodium spp*. in birds in tropical Asia; however, other genera of avian blood parasites have not been studied there. Additionally, no studies have characterized avian malarial parasites in Indochina, including Vietnam, an area very rich in biodiversity and endemism (Nhat 2001). Given these conservation concerns and a paucity of information on avian blood parasites in birds in Vietnam, my fourth Chapter was aimed at

characterizing the sample prevalence of avian blood parasites that cause avian malaria and investigating the ecological factors including habitat type, sampling region, flocking behavior, and age affecting prevalence in free-ranging wild land birds. I focused on two genera of blood parasites including *Plasmodium spp*. and *Haemoproteus spp*. that cause malaria in birds.

Avian influenza (AI) viruses are currently considered one of the most important bird-associated groups of zoonotic pathogens. This is in large part because of the attention drawn to birds from the high levels of culling and disease-associated mortality resulting from recent outbreaks of highly pathogenic avian influenza (HPAI) viruses of the H5N1 subtype. HPAI H5N1 has been implicated as the cause of mortality in a variety of wild bird species (Ellis et al. 2004, Kelly et al. 2008, Khan et al. 2009, Zhou et al. 2006). HPAI H5N1 has also killed wild mammals in captivity (Amonsin et al. 2006, Keawcharoen et al. 2004, Roberton et al. 2006) and has been responsible for illness and substantial mortality in humans, including 110 human cases in Vietnam, resulting in the deaths of 55 people (WHO 2009).

Due to the roles wild birds may play as reservoirs or as transmission bridges between organisms, and because they are directly threatened by HPAI H5N1, many wild bird populations have been surveyed for AI viruses globally (e.g.,Gaidet et al. 2007, Iverson et al. 2008, Lei et al. 2007). While AI viruses in general, and HPAI H5N1 in particular, have been detected in wild birds, most affected species inhabit wetlands or aquatic habitats (Olsen et al. 2006, Stallknecht and Brown 2007) such that land bird species are not currently considered important reservoirs of HPAI H5N1. Emerging evidence indicates that land birds could play an important role in preserving and

circulating HPAI H5N1 in the enviroment (Gronesova et al. 2008, Kou et al. 2005, Peterson et al. 2008). However, little information is available about the occurrence of AI viruses in land birds, especially in Southeast Asia including Vietnam, an area that is experiencing a relatively high incidence of outbreaks in humans and domestic poultry (Alexander 2007b, Hien et al. 2009). To begin to fill this information gap, in the fifth Chapter I focused on surveillance for the presence of AI virus nucleic acids and antibodies for AI viruses in free-ranging wild land birds in northern Vietnam. My study also sets the stage to investigate potential biological and ecological factors that regulate the presence of AI viruses in forest ecosystems.

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#### **CHAPTER 1**

# AN ASSESSMENT OF THE AVIAN CONSERVATION POTENTIAL OF PINE PLANTATIONS, SECONDARY GROWTH, AND MATURE NATURAL FORESTS IN TAM DAO NATIONAL PARK, VIETNAM

Abstract: The reduction of natural forest cover worldwide is a current cause of concern. Declines in natural forest cover have been observed in Southeast Asia including Vietnam, leading to the local extinction of many bird populations. Recently overall forest cover in Vietnam has increased, but most of the increase has been attributed to plantations of non-native trees, and natural forest is still being reduced and replaced by other land uses, such as plantations. The conservation value of these plantations for birds is unknown. My objective is to examine the avian conservation potential of pine plantations, compared to other natural vegetation types including secondary growth forests and mature forests, by estimating species richness in these different vegetation types. The study area was in Tam Dao National Park, northern Vietnam. Two observers surveyed bird communities along transects in the three forest types: mature forest, secondary growth forest and pine plantation over six sessions during summer 2006. Bird species were classified into two categories: forest specialists or forest generalists. Total species richness and number of species in each category were estimated using the Pledger-Huggins estimator with two mixtures. Regional commonness index, singing

propensity, and body length were used to model the heterogeneity in detection probability among species. In every analysis, detection probabilities in the two mixtures were substantially different. Regional commonness index and singing propensity had the most influence on probability of detection. For forest specialists, detection probability was highest in mature forest, lower in secondary growth forest, and lowest in pine plantation. For generalists, detection probability was highest in pine plantation, lower in secondary growth forest and least in mature forest. I estimated total species richness and number of forest specialist species to be highest in mature forest (143.88; 95% CI = 95.23, 192.54, and 88.08; 95% CI = 46.94, 129.22 respectively), lower in secondary growth (111.99 (95% CI = 75.47, 148.51 and 57.51; 95% CI = 17.51, 97.51 respectively), and lowest in pine plantation (83.24; 95% CI = 53.75, 112.74 and 49.45; 95% CI = 1.84, 97.06 respectively). The number of forest generalist species was estimated to be similar between mature forest and secondary growth forest (103.28; 95% CI = 17.24, 189.31 and 100.41; 95% CI = 42.36, 158.47, respectively) and least in pine plantation (56.57; 95% CI = 31.28, 81.85). I suggest that natural forest types should receive priority for conservation in Vietnam and pine plantations should be managed to provide additional structure in hopes of increasing avian species richness.

## **INTRODUCTION**

The extreme reduction of natural forest cover worldwide is a current cause of concern (Collar et al. 1994, Sodhi et al. 2008). Declines in natural forest cover have been observed in Southeast Asia, including Vietnam, leading to the local extinction of many bird populations (Sodhi and Brook 2006). Recently, overall forest cover in Vietnam has increased, but most of the increase has been attributed to plantations of non-native trees, and natural forests are still being reduced and replaced by other land uses (Nhat 2001). The conservation value of these plantations for birds is unknown although few natural forest bird species are assumed to persist in other land uses (Hughes et al. 2002). For tree plantations, this may be due to the low structural complexity resulting from the uniform age and physiognomy of the plantation trees and poorly developed understory, leading to lower abundance of food items and fewer opportunities for concealment (Kwok and Corlett 2000). In general, bird species diversity is reported to be positively correlated with vegetation structure and composition (MacArthur and MacArthur 1961, Wiens 1992). Recent evidence suggests that some land uses, such as tree plantations, can have great potential for forest bird species conservation, especially with management practices that diversify the forest vegetation and composition (Reitsma et al. 2001, Beukema et al. 2007).

Managing industrial forests in Vietnam for the dual purposes of wood production and conservation is of wide national interest in Vietnam. The recently proposed plan "Five Million Hectares of Forest" (Vietnam Government 1998) would increase the forest cover nationwide in Vietnam from 33% to 45% by planting non-native tree plantations. Overall benefits of this plan will be enhanced if conservation values can be incorporated into economic concerns. My objective is to examine the avian conservation potential of pine plantations compared to other natural vegetation types including secondary growth forests and mature forests.

Specifically, I will test several predictions relating patterns of species richness with forest types. Natural forest has very complex vegetation and structure, and is hypothesized to support a larger number of bird species than plantation forests. Therefore I predict that total species richness will be highest in mature forest and lower in secondary growth forest and pine plantations. Beyond overall richness, I will examine predictions concerning forest specialist and forest generalist species guilds. Forest specialists are bird species that are intolerant to forest disturbances. Forest generalists are bird species that inhabit all forest types and are tolerant to forest disturbances. I predict that forest specialist species richness will be higher in mature forest than the other two vegetation types and that forest generalist species will be equally rich in mature forests, secondary forests and pine plantations.

#### **METHODS**

#### Study area

The study area was in Tam Dao National Park (TDNP), Vietnam  $(21^{\circ} 21^{\circ} - 21^{\circ} 42^{\circ} \text{ N}; 105^{\circ} 23^{\circ} - 105^{\circ} 44^{\circ} \text{ E})$ . The main part of TDNP is in the Tam Dao mountain range with the highest peak reaching 1,590 m. The park is 10-15 km wide, 80 km long, and located in 3 provinces: Thai Nguyen, Tuyen Quang, Vinh Phuc. The Park center is 70 km northwest of the capital, Hanoi (Appendix I).

The climate in TDNP is tropical with two distinctive seasons caused by monsoon winds. The hot and rainy season is from May to November, the cold and dry season is from December through April. Average year-round temperature is 23.3°C, with a minimum temperature of 1.8°C, and the maximum temperature is 41.5°C. The park receives ~16 cm precipitation and relative humidity averages 82%.

TDNP supports a very large number of plant species including at least 904 species of higher plants and a large number of animal species, including at least 239 birds, many of which are rare or endangered. The study area was located on the south-west slope of the Tam Dao range. Sampled forest areas ranged from 200 to 600 m in elevation. The natural vegetation in this area can be divided in two types, mature forest and secondary growth forest. Mature forest may have had some selective logging in the past, but the forest remains intact with three canopy layers, and with a top canopy height of 30-40 m. Secondary growth forest results from intense logging and wood gathering. Secondary growth forest vegetation is comprised of only small trees, with forest height usually less than 10 m. The Tam Dao area also contains about 1,500 ha of pine plantation primarily planted in one main plantation as well as in some small fragments. The pine plantation is about 30-50 years old.

## Avian sampling

Birds were surveyed in the three forest types (strata): mature forest, secondary growth forest, and pine plantation. Sampling effort, both in terms of person-hours and area sampled, was approximately the same in all three strata. Sampling effort was similar

among strata to reduce the effects of an area-species richness relationship and sampling variability on comparisons of species richness among vegetation types.

All possible 500 m transects were designated on a map of the study area. Transects were chosen to be at least 75 m from any forest edge to minimize any edge effect. Transects were also separated by at least 100 m to insure independence among transects. From a random start point, 12 transects were systematically selected in each vegetation type.

Transects were surveyed six times from June to August 2006. Surveys were carried out under favorable weather conditions. Surveys were conducted from sunrise to noon. Observers walked transects at a constant speed of ~0.5km/40 minutes. While walking transects, observers recorded the species of all birds heard and/or seen except for birds flying overhead which were not recorded. Bird species were classified into two categories: forest specialist or forest generalist following Robson (2005) and Cu et al. (2000).

#### **Data Analysis**

Many species richness estimators have been developed, almost all are preferable to conventional 'observed number of species' (Walther and Morand 1998, Walther and Moore 2005) and much emphasis has been placed on the use of jackknife estimators (Burnham and Overton 1978) and Chao estimators (Chao 1984, Chao 1987). However the jackknife and Chao estimators are not based on a maximum-likelihood framework (Walther and Moore 2005); therefore, robust model selection and model uncertainty measurements, including model averaging (Burnham and Anderson 2002) cannot be

utilized. These estimators also do not allow the modeling of individual covariates. Individual covariates such as relative abundance, singing propensity, or visual appearance may be expected to explain much of the individual heterogeneity in individual species detection probability. More recently the Huggins estimator (Huggins 1991) has been developed for abundance estimation, but has not yet seen much use in species richness applications. The Huggins estimator is based on maximum likelihood theory and also allows the use of individual species covariates in modeling detection probability. Additionally, Pledger (2000) developed a model partitioning individuals into finite groups of relatively homogeneous capture probabilities. This model has been used in closed capture-recapture abundance studies (Williams et al. 2002). Heterogeneity in capture (or detection) probability is believed to be more important at a community level (e.g., species-richness; Nichols et al. 1998) than at a population level (e.g., abundance) and the heterogeneity in detection cannot be explained fully by individual covariates. Because of these advantages of the Huggins and Pledger models, I used an estimator that combines these two models.

I estimated overall species richness, as well as the number of forest specialist and forest generalist species in Program MARK (White and Burnham 1999). Data from the 12 transects from one survey period were pooled within vegetation type and survey period and treated as a single sampling occasion (for a total of 6 sampling occasions). Encounter histories were constructed for all bird species detected during the surveys. Due to data sparseness and preliminary modeling, two mixtures were used for modeling detection probability with a common probability of inclusion in each mixture across habitat types. Pledger (2000) suggests that using two mixtures is enough to substantially
correct for heterogeneity-induced bias in estimation of population size (or in my case species richness).

Regional commonness (co), singing propensity (si) and body length (bo) (Table 1.1, Appendix II) were used as covariates to test predictions concerning detection probabilities. I thought 'regional commonness' might have a quadratic relationship with detection probability because the detection probability does not depend much on abundance if abundance is high. Information used to develop the regional commonness index of each species and information on the body length was inferred from previous avian surveys conducted in TDNP in 2005 (Davidson et al. 2005), and from Robson (2005) and Cu et al. (2000). Singing propensity was used as an indicator variable in which bird species that can be recognized easily by their typical songs and sing often (covariate value of 1) were compared with species that are not as easy to detect by song (covariate value of 0). Relationships between body length, singing propensity and detection probability were assumed to be linear.

The importance of these covariates in modeling detection probabilities, as well as vegetation types, was examined using model ranking ( $\Delta$ AICc), cumulative AICc weights ( $\Sigma w_i$ ), and by examining parameter estimates (Burnham and Anderson 2002). Specifically, the main candidate models were: (1) equal detection probabilities (P) in the three vegetation types ( $P_{MF=SG=PP}$ ) (MF = mature forest, SG = secondary growth forest, and PP = pine plantation); (2) equal detection probabilities in mature forests and secondary growth, with pine plantations being different ( $P_{MF=SG=PP}$ ); (3) equal detection probabilities in secondary growth forest and pine plantations, with mature forest being different ( $P_{MF=SG=PP}$ ); and (4) different detection probabilities for each of the three

vegetation types ( $P_{MF\#SG\#PP}$ ). In addition to habitat types, I also modeled detection probabilities as a function of survey occasion (t) in an additive (+) and interactive (\*) way. With each of these models I also added covariate effects of observer (ob), singing propensity (si), body length (bo), and regional commonness index (co) separately or in combination. A total of 128 models were constructed for each analysis of total species richness, number of forest specialist species, and number of forest generalist species. Parameters of interest were model-averaged across the entire model set.

# RESULTS

#### Raw data

Observers recorded 3648 individual birds. Seventy one, 60, and 45 avian species were detected in mature forest, secondary-growth forest, and pine plantations, respectively. These species belong to 8 orders and 21 families. The families Sylviidae, Corvidae, Pycnonotidae, and Nectariniidae were most frequently observed. The most frequently observed species were: Common Tailorbird (*Orthotomus sutorius*), Puff-throated Bulbul (*Alophoixus pallidus*), Red-whiskered Bulbul (*Pycnonotus jocosus*), Grey-cheeked Fulvetta (*Alcippe morrisonia*), Striped Tit-Babbler (*Macronous gularis*), Buff-breasted Babbler (*Pellorneum tickelli*), and Puff-throated Babbler (*Pellorneum ruficeps*). The entire species list is given in Appendix II. Out of 98 species detected, 49 species were classified as forest specialists and 49 species were classified as generalists. Forty six, 24, and 14 forest specialist species were detected in mature forest, secondary-growth forest, and pine plantation, respectively. Twenty five, 36, and 31 forest generalist

species were detected in mature forest, secondary growth forest, and pine plantation, respectively.

# **Total species richness**

Models in which detection probability varied by observer ranked highly, all top models with  $\Delta AICc < 2.00$  consistently contained the observer effect (Table 1.2). Models in which detection varied with time, either additively or multiplicatively with habitat types were ranked lower, with all models containing time effects having  $\Delta AICc >$ 7.00 and AICc weight ( $w_i$ ) < 0.01. Models without a time effect were always selected over models incorporating a time effect. Detection probabilities in the two mixtures were substantially different (Fig. 1.1), thus there were two groups of species: one group had high detection probabilities and the other very low detection probabilities due to unknown individual heterogeneity in detection probability. Twenty six percent (95% CI = 18%, 35%) of the species belonged to the high detection group.

Regional commonness index had the most support in explaining variation in detection probability with cumulative AICc weight  $(\Sigma w_i) = 1.00$ . Models with  $w_i > 0.01$  consistently contained the regional commonness index and models using regional commonness index as a single individual covariate were always selected over models using singing propensity or body length as single individual covariate. Regional commonness index and singing propensity had a positive relationship with detection probability (Fig. 1.2). Singing propensity also influenced detection probabilities ( $\Sigma w_i = 0.87$ ). Body length had the least influence on detection probability ( $\Sigma w_i = 0.33$ ).

Based on model averaging results, I estimated species richness to be 143.88 (95% CI = 95.23, 192.54) in mature forest, 111.99 (95% CI = 75.47, 148.51) in secondarygrowth forest, and 83.24 (95% CI = 53.75, 112.74) in the pine plantation (Fig. 1.3).

#### **Forest specialist species**

Models in which detection varied by habitat types had strong explanatory ability, with habitat effects incorporated into all models with  $w_i > 0.01$  (Table 1.3). Models incorporating habitat effects were always selected over models not incorporating habitat effects. Detection probability was highest in mature forest, lower in secondary growth forest, and least in pine plantation (Fig. 1.4). Models with time-varying detection probability did not have much explanatory value (Table 1.3). All models containing time effects had  $\Delta AICc > 5.00$  and AICc weight ( $w_i$ ) < 0.01. Detection probabilities in two mixtures were substantially different (Fig. 1.4) indicating that some species (31%; 95% CI = 18%, 47%) were highly detectable and the rest had low detection probabilities.

Regional commonness index ( $\Sigma w_i = 1.00$ ) had the most influence on detection probability, and consistently appeared in the top models (Table 1.3 and Fig. 1.5). Singing propensity ( $\Sigma w_i = 0.52$ ) had weaker influence on detection probability (Fig. 1.5) and body length ( $\Sigma w_i = 0.45$ ) had the least influence on detection probability, only occasionally appearing in the top models.

Based on model averaging results, I estimated number of forest specialist species to be 88.08 (95% CI = 46.94, 129.22) in mature forest, 57.51 (95% CI = 17.51, 97.51) in secondary-growth forest, and 49.45 (95% CI = 1.84, 97.06) in pine plantations (Fig. 1.3).

# **Forest generalist species**

Models in which detection varied by habitat had strong support; all top models with low  $\Delta$ AICc values contained habitat effects (Table 1.4). Models incorporating observer and/or habitat effects were always selected over models not incorporating these effects. Detection probability was highest in pine plantation, lower in secondary growth forest, and lowest in mature forest (Fig. 1.6). Models with time-varied detection probability did not have much explanatory value. All models containing time effect have  $\Delta$ AICc > 6.00 and AICc weight ( $w_i$ ) < 0.02 (Table 1.4). Detection probabilities in two mixtures were substantially different (Fig. 1.6) indicating that some species (26%; 95% CI = 15%, 41%) were highly detectable and the rest had low detection probabilities.

All three covariates, regional commonness index ( $\Sigma w_i = 1.00$ ), singing propensity ( $\Sigma w_i = 1.00$ ), and body length ( $\Sigma w_i = 0.86$ ) had explanatory ability as some top models incorporate all three of these covariates. Regional commonness index was the best in explaining the variation in detection probability; all models with  $w_i > 0.01$  consistently contained regional commonness index (Table 1.4 and Fig. 1.7). Singing propensity consistently appeared in the top models and was the second best explanatory covariate (Table 1.4 and Fig. 1.7). Body length had weaker influence on detection probabilities than regional commonness index and singing propensity, and was less frequently in the top models.

Based on model-averaged results, I estimated number of forest generalist species to be 103.28 (95% CI = 17.24, 189.31) in mature forest, 100.41 (95% CI = 42.36, 158.47) in secondary-growth forest, and 56.57 (95% CI = 31.28, 81.85) in pine plantation (Fig. 1.3).

#### DISCUSSION

#### **Detection probability**

In all analyses, a two-point mixture model described detection probabilities well and the estimates for the 2 mixtures were substantially different. Models without mixtures were also run in a pre-analysis and had much higher AICc values suggesting that models incorporating mixtures would better describe bird detection probabilities. Species varied greatly in their detection probabilities and although the covariates model some of this heterogeneity, the mixture structure was also needed. Unmodeled heterogeneity in detection could have been influenced by other factors (e.g., color, behavior) and the Pledger model was useful in describing this unmodeled heterogeneity. 25-31% of species can be categorized as having a high detection probability, while the rest have a very low detection probability. Although some top models contain observer effects, upon further inspection the differences between the observers were minimal.

Regional commonness index had a large influence on detection probabilities ( $\Sigma w_i$ = 1 in all three analyses). The probability of detecting a species will increase with increases in individual species abundances (Royle and Nichols 2003) and my regional commonness index and the combination of linear and quadratic terms of regional commonness index probably captured this relationship well. Singing propensity had the second best explanatory ability. In the analysis of forest specialists ( $\Sigma w_i = 0.52$ ), the effect of singing propensity is much lower than in the other two analyses ( $\Sigma w_i = 0.90$  and 1.00). This result is perhaps due to the fact that observers were less familiar with the songs of forest specialist species than those of forest generalist species. Body length had little explanatory ability. Visual cues are not the only way species are detected. Although species with large body size are generally more easily seen than the small ones, most large species forage solitarily during the breeding season, thus making their detection lower than the small species that forage in flocks. These aspects probably made body length a poorer predictor of detection probability.

Detection probabilities varied strongly by habitat types in the estimation of number of forest specialist and forest generalist species. This is partially due to detection probabilities being possibly influenced by abundance (sensu Royle and Nichols 2003) which was scored as regional commonness index in my study. Forest specialist species may be more abundant in mature forest than in secondary growth forest and pine plantations making the species detection probabilities in mature habitat higher than in other habitat types in the analysis of forest specialist species (Fig. 1.4). In contrast, forest generalist species may be more abundant in secondary growth forests and pine plantations than in mature forests. Therefore, in the analysis of forest generalists, detection probabilities in secondary growth forests and pine plantations were higher than in mature forests (Fig. 1.6). These two relationships probably balance each other out when all species were considered in the species richness analysis. In this analysis, habitat had much smaller effects (Fig. 1.1). Although forest generalist species may be more abundant in secondary growth forest than in pine plantation, detection in pine plantation was still slightly higher than in secondary growth forest. This higher detection probability in pine plantation was likely attributed to better visibility in this habitat. Detection probabilities also did not vary by time possibly because all surveys were conducted during similar conditions.

# **Species richness**

Species richness was highest in mature forest, less in secondary growth forest and least in pine plantation although 95% confidence intervals for estimates in mature forest compared to secondary growth forest and secondary growth forest compared to pine plantation overlap. The number of forest generalist species seems to be similar between mature forest and secondary growth forest and lower in pine plantation. My results are similar to those reported in several studies conducted within a variety of plantations (Greenberg et al. 1997; Raman and Sukumar 2002; Cockle et al. 2005; Rotenberg 2007). The number of forest specialist species was also highest in mature forest and less in secondary growth and least in pine plantations. Although some studies found similar total species richness in natural forest and plantations, the number of forest specialist species was always higher in natural forest (Kwok and Corlett 2000, Reitsma et al. 2001). Secondary growth may have lower species richness due to lower overall canopy height and fewer canopy layers, and due to the history of logging, wood gathering, and cattle grazing. Pine plantations may have lower species richness due to the lack of tree species diversity and tree-age diversity. Since habitat structure complexity and diversity have been reported to be highly correlated with bird species richness (MacArthur and MacArthur 1961, Wiens 1992), the lower tree diversity and complexity may directly lead to lower diversity in fructivorous, granivorous, and nectarivorous bird species. Only 50% of the total species detected used pine canopy as foraging habitat, and no fructivorous species were detected in pine plantations in my study. There are seven species that are not found in the other forest types except for pine plantations, five of which are possibly

not observed in other habitat types just by chance alone. Other two species are open country species. No species detected is unique to the pine plantations.

The pine plantation understory may also be poorer than the other vegetation types for many avian species because pine leaves contain oils that creates a barrier on the forest floor, not letting seeds reach soils and inhibiting the regrowth and development of shrubs and native trees. Cockle et al. (2005) also found a similar result with the absence of forest understory and forest floor bird species in plantations in Paraguay. The absence of fructivorous avian species, in turn, inhibits seed dispersal in pine plantations. In the area where pine density is low or where gaps created by fallen pine trees are common, the understory development appears to be much better than in dense, young pine stands (T. Vu, per. obs.).

The pine plantation canopy is more permeable to light due to pine's needlelike leaves, causing the microclimate in the pine plantation understory to be drier than those under mature forest and secondary-growth forest. Besides low plant diversity, the drier habitat in pine plantation may make it an unfavorable environment to support high abundance of invertebrates, especially arthropods on the forest floor. This may reduce the overall insectivorous species and ground-feeding insectivores in pine plantations.

The availability of cavities and snags in secondary growth is less than in mature forest because secondary growth does not have old and large stems. Pine plantations also lack cavities because of forest management practices. Therefore, the smaller overall species richness and fewer numbers of forest specialist species in secondary growth and pine plantations may also be attributed to the reduction of cavity nesting and stem foraging species (Schwab et al. 2006, Tomasevic and Estades 2006). For example, seven

woodpecker species were detected in mature forest, whereas only one species was detected in secondary growth and two species were detected in pine plantation.

# **Management Implications**

Avian conservation value is highest in mature and secondary-growth forests and least in pine plantations. Although pine plantations can support a number of species, most of these species are not forest specialists. No species detected is unique to the pine plantations. Besides commercial plantations, exotic trees are also being planted in the national parks and watersheds in mountainous areas to prevent soil erosion, floods, and to manage the water quality and quantity in reservoirs, streams, and rivers. I recommend that where the natural succession is possible and wood production is not a major concern, natural forests should be preserved and natural regeneration be promoted. Thinning practices should be implemented in existing pine plantations to create more openings for natural trees to regenerate and develop undergrowth and to diversify the age structure of the forest. Forest enrichment with more native trees within pine plantations should also be considered.

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Covariate	Description	Range	Mean ± SD
Body length (bo, cm)	Taken from Robson (2005).	ALL: 8.50 - 67.00 MF: 8.70 - 56.00 SG: 8.50 - 62.00 PP: 8.70 - 67.00	ALL: $21.79 \pm 10.85$ MF: $21.40 \pm 8.51$ SG: $20.32 \pm 10.78$ PP: $24.37 \pm 13.76$
Regional commonness index (co)	Scored according to 5 categories of abundance common - 5, fairly common - 4, uncommon - 3, scarce - 2, rare - 1. Scoring was inferred from Davison et al. (2005), Robson (2005) and Cu et al. (2000) and prior experience.	ALL: 1 - 5 MF: 1 - 5 SG: 1 - 5 PP: 1 - 5	ALL: $3.33 \pm 1.50$ MF: $3.25 \pm 1.61$ SG: $3.33 \pm 1.54$ PP: $3.33 \pm 1.26$
Singing propensity (si)	Species that can be recognized easily during the survey by their typical calls or songs and tend to sing often have value 1, all others have value 0.	ALL: 0 - 1 MF: 0 - 1 SG: 0 - 1 PP: 0 - 1	ALL: $0.79 \pm 0.41$ MF: $0.74 \pm 0.44$ SG: $0.83 \pm 0.38$ PP: $0.80 \pm 0.40$

Table 1.1. Individual covariates used in modeling detection probabilities (MF=mature forest, SG=Secondary growth forest, PP=Pine plantation, and ALL = all habitats combined).

Table 1.2. Total species richness model selection results for 128 models describing detection probabilities in three habitats (MF=mature forest, SG=Secondary growth forest, and PP=Pine plantation) and two observers (ob). Two mixtures were used with a common probability of inclusion ( $\pi$ ) in each mixture across habitat types. Detection probability was models as equal in the three habitats ( $P_{MF=SG=PP}$ ), as equal in the mature and secondary growth forests only (P<sub>MF=SG#PP</sub>), as equal in the secondary growth and pine plantations only (P<sub>MF#SG=PP</sub>), as different for all forest types (P<sub>MF#SG#PP</sub>). The covariates (bo=body length, co=regional commonness index, and si=singing propensity) were also used to model detection probability separately or in combination. In addition to habitat types and other covariates, I also modeled detection probabilities as a function of survey occasion (t) in an additive (+) and interactive (\*) way. Models are ranked by AICc.  $\Delta AIC_c$  is the difference in AIC<sub>c</sub> units from the highest ranking model. AIC<sub>c</sub> weights ( $w_i$ ), model likelihood (L), number of parameters (K), and deviance (D) are also shown. AICc weights sum to one and models with higher likelihood have more weight. Model likelihood is the likelihood of a model relative to the other models. Deviance is the difference in  $(-2\log \times \text{likelihood})$  of the current model and  $(-2\log \times \text{likelihood})$  of the saturated model.

Model	AICc	∆AICc	Wi	L	K	D
P(MF=SG=PP, ob, co, si)	1208.82	0.00	0.21	1.00	7	1194.71
P( <sub>MF=SG#PP</sub> , ob, co, si)	1209.61	0.79	0.14	0.67	8	1193.47
P( <sub>MF=SG=PP</sub> , ob, co, si, bo)	1210.20	1.38	0.10	0.50	8	1194.06
P(MF#SG=PP, ob, co, si)	1210.76	1.94	0.08	0.38	8	1194.62
P( <sub>MF=SG#PP</sub> , ob, co, si, bo)	1210.84	2.02	0.08	0.36	9	1192.67
P(MF#SG#PP, ob, co, si)	1211.45	2.63	0.06	0.27	9	1193.28
P( <sub>MFF#SG=PP</sub> , ob, co, si, bo)	1212.10	3.28	0.04	0.19	9	1193.93
P( <sub>MFF=SG=PP</sub> , ob, co)	1212.15	3.33	0.04	0.19	6	1200.07
P( <sub>MFF=SG=PP</sub> , co, si)	1212.25	3.43	0.04	0.18	6	1200.17
P(MF#SG#PPPP, ob, co, si, bo)	1212.72	3.90	0.03	0.14	10	1192.51
P( <sub>MF=SG#PP</sub> , co, si)	1213.06	4.24	0.02	0.12	7	1198.95
P( <sub>MF=SG=PP</sub> , co, si, bo)	1213.63	4.81	0.02	0.09	7	1199.52
P( <sub>MF=SG#PP</sub> , ob, co)	1213.92	5.10	0.02	0.08	7	1199.82
$P(_{MF=SG=PP}, ob, co, bo)$	1214.02	5.20	0.02	0.07	7	1199.91
P( <sub>MF#SG=PP</sub> , ob, co)	1214.04	5.22	0.02	0.07	7	1199.93
P( <sub>MF#SG=PP</sub> , co, si)	1214.19	5.37	0.01	0.07	7	1200.08
P( <sub>MF=SG#PP</sub> , co, si, bo)	1214.29	5.47	0.01	0.07	8	1198.15
P( <sub>MF#SG#PP</sub> , co, si)	1214.90	6.08	0.01	0.05	8	1198.76
P( <sub>MF#SG=PP</sub> , co, si, bo)	1215.53	6.71	0.01	0.03	8	1199.39
$P(_{MF=SGG=PP}, co)$	1215.53	6.71	0.01	0.03	5	1205.48
P( <sub>MF=SGG#PP</sub> , ob, co, bo)	1215.69	6.87	0.01	0.03	8	1199.56
P( <sub>MF#SG=PPPP</sub> , ob, co, bo)	1215.86	7.04	0.01	0.03	8	1199.72
P( <sub>MF#SG#PPPP</sub> , ob, co)	1215.93	7.11	0.01	0.03	8	1199.79

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Model	AICc	∆AICc	Wi	L	K	D
P( <sub>MF#SG#PP</sub> , co, si, bo)	1216.17	7.35	0.01	0.03	9	1198.00
$P(_{MF=SG=PP}, +t, co, si)$	1216.55	7.73	0.00	0.02	11	1194.29
$P(_{MF=SG\#PP}, co)$	1217.31	8.49	0.00	0.01	6	1205.23
$P(_{MF=SG\#PP}, +t, co, si)$	1217.35	8.53	0.00	0.01	12	1193.05
$P(_{MF=SG=PP}, co, bo)$	1217.40	8.58	0.00	0.01	6	1205.32
P( <sub>MF#SG=PP</sub> , co)	1217.42	8.60	0.00	0.01	6	1205.34
P( <sub>MF#SG#PP</sub> , ob, co, bo)	1217.68	8.86	0.00	0.01	9	1199.51
$P(_{MF=SG=PP}, +t, co, si, bo)$	1217.94	9.12	0.00	0.01	12	1193.64
$P(_{MF\#SG=PP}, +t, co, si)$	1218.50	9.68	0.00	0.01	12	1194.20
$P(_{MF=SG\#PP}, +t, co, si, bo)$	1218.59	9.77	0.00	0.01	13	1192.25
$P(_{MF=SG\#PP}, co, bo)$	1219.08	10.26	0.00	0.01	7	1204.97
P( <sub>MF#SG#PP</sub> , +t, co, si)	1219.20	10.38	0.00	0.01	13	1192.85
P( <sub>MF#SG=PP</sub> , co, bo)	1219.24	10.42	0.00	0.01	7	1205.13
P( <sub>MF#SG#PP</sub> , co)	1219.31	10.49	0.00	0.01	7	1205.20
$P(_{MF=SG=PP}, +t, co)$	1219.86	11.04	0.00	0.00	10	1199.65
$P(_{MF\#SG=PP}, +t, co, si, bo)$	1219.86	11.04	0.00	0.00	13	1193.51
P( <sub>MF#SG#PP</sub> , +t, co, si, bo)	1220.49	11.67	0.00	0.00	14	1192.09
P( <sub>MF#SG#PP</sub> , co, bo)	1221.06	12.24	0.00	0.00	8	1204.92
$P(_{MF=SG\#PP}, +t, co)$	1221.65	12.83	0.00	0.00	11	1199.40
$P(_{MF=SG=PP}, +t, co, bo)$	1221.75	12.93	0.00	0.00	11	1199.50
$P(_{MF\#SG=PP}, +t, co)$	1221.77	12.95	0.00	0.00	11	1199.52
$P(_{MF=SG\#PP}, +t, co, bo)$	1223.44	14.62	0.00	0.00	12	1199.14
$P(_{MF\#SG=PP}, +t, co, bo)$	1223.60	14.78	0.00	0.00	12	1199.30
$P(_{MF\#SG\#PP}, +t, co)$	1223.67	14.85	0.00	0.00	12	1199.37
$P(_{MF\#SG\#PP}, +t, co, bo)$	1225.44	16.62	0.00	0.00	13	1199.09
P( <sub>MF=SG=PP</sub> , *t, co, si)	1228.52	19.70	0.00	0.00	21	1185.63
P( <sub>MF=SG=PP</sub> , *t, co, si, bo)	1229.76	20.94	0.00	0.00	22	1184.78
P( <sub>MF#SG=PP</sub> , *t, co, si)	1230.07	21.25	0.00	0.00	22	1185.09
P( <sub>MF=SG#PP</sub> , *t, co, si)	1230.42	21.60	0.00	0.00	22	1185.44
P( <sub>MF#SG=PP</sub> , *t, co, si, bo)	1231.40	22.58	0.00	0.00	23	1184.33
P( <sub>MF=SG#PP</sub> , *t, co, si, bo)	1231.72	22.90	0.00	0.00	23	1184.65
P( <sub>MF#SG#PP</sub> , *t, co, si)	1232.15	23.33	0.00	0.00	23	1185.08
$P(_{MF=SG=PP}, *t, co)$	1233.14	24.32	0.00	0.00	20	1192.33
P( <sub>MF#SG#PP</sub> , *t, co, si, bo)	1233.49	24.67	0.00	0.00	24	1184.33
$P(_{MF=SG\#PP}, *t, co)$	1234.65	25.82	0.00	0.00	21	1191.75
$P(_{MF=SG=PP}, *t, co, bo)$	1234.80	25.98	0.00	0.00	21	1191.91
$P(_{MF\#SG=PP}, *t, co)$	1234.94	26.12	0.00	0.00	21	1192.05
$P(_{MF=SG\#PP}, *t, co, bo)$	1236.44	27.62	0.00	0.00	22	1191.46
$P(_{MF\#SG\#PP}, *t, co)$	1236.68	27.86	0.00	0.00	22	1191.71
P( <sub>MF#SG=PP</sub> , *t, co, bo)	1236.69	27.87	0.00	0.00	22	1191.71
$P(_{MF\#SG\#PP}, *t, co, bo)$	1238.50	29.68	0.00	0.00	23	1191.43

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Model	AICc	∆AICc	Wi	L	K	D
P( <sub>MF=SG#PP</sub> , ob)	1238.76	29.93	0.00	0.00	5	1228.70
P( <sub>MF=SG#PP</sub> , ob, bo)	1239.06	30.24	0.00	0.00	6	1226.98
P( <sub>MF=SG#PP</sub> , ob, si, bo)	1239.95	31.13	0.00	0.00	7	1225.85
P( <sub>MF#SG#PP</sub> , ob)	1240.28	31.46	0.00	0.00	6	1228.20
P( <sub>MF#SG#PP</sub> , ob, si, bo)	1240.83	32.00	0.00	0.00	8	1224.69
$P(_{MF=SG\#PP})$	1242.23	33.41	0.00	0.00	4	1234.19
$P(_{MF=SG=PP}, ob)$	1242.23	33.41	0.00	0.00	4	1234.20
$P(_{MF=SG\#PP}, +t, si, bo)$	1242.50	33.68	0.00	0.00	11	1220.25
P( <sub>MF=SG#PP</sub> , bo)	1242.56	33.74	0.00	0.00	5	1232.50
P( <sub>MF=SG=PP</sub> , ob, bo)	1243.02	34.20	0.00	0.00	5	1232.97
P( <sub>MF#SG=PP</sub> , ob, si, bo)	1243.06	34.24	0.00	0.00	7	1228.95
P( <sub>MF=SG#PP</sub> , si, bo)	1243.27	34.45	0.00	0.00	6	1231.19
P( <sub>MF#SG#PP</sub> )	1243.79	34.97	0.00	0.00	5	1233.73
P( <sub>MF#SG#PP</sub> , ob, bo)	1243.89	35.06	0.00	0.00	7	1229.78
P( <sub>MF#SG#PP</sub> , si, bo)	1244.14	35.32	0.00	0.00	7	1230.04
$P(_{MF\#SG=PP}, ob)$	1244.23	35.41	0.00	0.00	5	1234.18
P( <sub>MF=SG=PP</sub> , ob, si, bo)	1244.39	35.57	0.00	0.00	6	1232.31
P( <sub>MF#SG#PP</sub> , bo)	1244.50	35.68	0.00	0.00	6	1232.42
P( <sub>MF=SG=PP</sub> , ob, si)	1245.59	36.77	0.00	0.00	5	1235.54
P( <sub>MF=SG=PP</sub> )	1245.75	36.93	0.00	0.00	3	1239.73
P( <sub>MF#SG=PP</sub> , ob, bo)	1246.12	37.30	0.00	0.00	6	1234.04
P( <sub>MF#SG=PP</sub> , si, bo)	1246.38	37.56	0.00	0.00	6	1234.30
$P(_{MF=SG\#PP}, +t)$	1246.44	37.62	0.00	0.00	9	1228.27
P( <sub>MF=SG=PP</sub> , bo)	1246.53	37.71	0.00	0.00	4	1238.50
$P(_{MF=SG\#PP}, +t, bo)$	1246.76	37.94	0.00	0.00	10	1226.55
P(MF#SG=PP, ob, si)	1247.39	38.57	0.00	0.00	6	1235.31
P( <sub>MF=SG#PP</sub> , ob, si)	1247.61	38.79	0.00	0.00	6	1235.53
P( <sub>MF=SG=PP</sub> , si, bo)	1247.71	38.89	0.00	0.00	5	1237.65
P( <sub>MF#SG=PP</sub> )	1247.75	38.92	0.00	0.00	4	1239.71
$P(_{MF\#SG\#PP}, +t)$	1247.98	39.16	0.00	0.00	10	1227.77
P( <sub>MF#SG#PP</sub> , +t, si, bo)	1248.58	39.75	0.00	0.00	12	1224.28
P( <sub>MF=SG=PP</sub> , si)	1248.97	40.15	0.00	0.00	4	1240.93
P( <sub>MF#SG=PP</sub> , bo)	1249.52	40.70	0.00	0.00	5	1239.47
P(MF#SG#PP, ob, si)	1249.61	40.79	0.00	0.00	7	1235.50
$P(_{MF=SG=PP}, +t)$	1249.90	41.08	0.00	0.00	8	1233.77
$P(_{MF=SG=PP}, +t, bo)$	1250.71	41.89	0.00	0.00	9	1232.54
P(MF#SG=PP, si)	1250.77	41.95	0.00	0.00	5	1240.71
P( <sub>MF=SG#PP</sub> , si)	1250.98	42.16	0.00	0.00	5	1240.92
$P(_{MF\#SG\#PP}, +t, bo)$	1251.61	42.79	0.00	0.00	11	1229.36
$P(_{MF\#SG=PP}, +t)$	1251.92	43.10	0.00	0.00	9	1233.75
P( <sub>MF#SG#PP</sub> , si)	1252.62	43.79	0.00	0.00	6	1240.54

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Model	AICe	ΔAICc	Wi	L	K	D
$P(_{MF=SG=PP}, +t, si)$	1253.29	44.47	0.00	0.00	9	1235.12
$P(_{MF\#SG=PP}, +t, bo)$	1253.83	45.01	0.00	0.00	10	1233.62
$P(_{MF\#SG=PP}, +t, si)$	1255.10	46.28	0.00	0.00	10	1234.89
$P(_{MF=SG=PP}, +t, si, bo)$	1255.12	46.30	0.00	0.00	10	1234.91
$P(_{MF=SG\#PP}, +t, si)$	1255.32	46.50	0.00	0.00	10	1235.11
$P(_{MF\#SG=PP}, +t, si, bo)$	1256.46	47.64	0.00	0.00	11	1234.21
$P(_{MF\#SG\#PP}, +t, si)$	1256.97	48.15	0.00	0.00	11	1234.72
$P(_{MF=SG=PP}, *t, si, bo)$	1257.79	48.97	0.00	0.00	20	1216.98
$P(_{MF=SG\#PP}, *t)$	1258.73	49.91	0.00	0.00	19	1220.00
$P(_{MF=SG\#PP}, *t, bo)$	1259.34	50.52	0.00	0.00	20	1218.53
P( <sub>MF#SG=PP</sub> , *t, si, bo)	1259.59	50.76	0.00	0.00	21	1216.69
P( <sub>MF=SG#PP</sub> , *t, si, bo)	1259.66	50.83	0.00	0.00	21	1216.76
P( <sub>MF#SG#PP</sub> , *t)	1260.74	51.92	0.00	0.00	20	1219.93
P( <sub>MF#SG#PP</sub> , *t, si, bo)	1261.61	52.79	0.00	0.00	22	1216.63
$P(_{MF=SG=PP}, *t)$	1263.29	54.46	0.00	0.00	18	1226.63
$P(_{MF=SG=PP}, *t, bo)$	1264.04	55.22	0.00	0.00	19	1225.31
$P(_{MF\#SG\#PP}, *t, bo)$	1264.09	55.27	0.00	0.00	21	1221.20
$P(_{MF\#SG=PP}, *t)$	1264.72	55.90	0.00	0.00	19	1225.99
P( <sub>MF=SG=PP</sub> , *t, si)	1266.34	57.52	0.00	0.00	19	1227.60
$P(_{MF\#SG=PP}, *t, bo)$	1267.35	58.53	0.00	0.00	20	1226.54
P( <sub>MF#SG=PP</sub> , *t, si)	1268.04	59.22	0.00	0.00	20	1227.23
P( <sub>MF=SG#PP</sub> , *t, si)	1268.37	59.55	0.00	0.00	20	1227.56
P( <sub>MF#SG#PP</sub> , *t, si)	1269.96	61.14	0.00	0.00	21	1227.07

Table 1.3. Model selection results for 128 models describing detection probabilities in three habitats (MF=mature forest, SG=Secondary growth forest, and PP=Pine plantation) and two observers (ob) for forest specialist species. Two mixtures were used with a common probability of inclusion ( $\pi$ ) in each mixture across habitat types. Detection probability was models as equal in the three habitats ( $P_{MF=SG=PP}$ ), as equal in the mature and secondary growth forests only (P<sub>MF=SG#PP</sub>), as equal in the secondary growth and pine plantations only (P<sub>MF#SG=PP</sub>), as different for all forest types (P<sub>MF#SG#PP</sub>). The covariates (bo=body length, co=regional commonness index, and si=singing propensity) were also used to model detection probability separately or in combination. In addition to habitat types and other covariates, I also modeled detection probabilities as a function of survey occasion (t) in an additive (+) and interactive (\*) way. Models are ranked by AICc.  $\Delta AIC_c$  is the difference in AIC<sub>c</sub> units from the highest ranking model. AIC<sub>c</sub> weights ( $w_i$ ), model likelihood (L), number of parameters (K), and deviance (D) are also shown. AICc weights sum to one and models with higher likelihood have more weight. Model likelihood is the likelihood of a model relative to the other models. Deviance is the difference in  $(-2\log \times \text{likelihood})$  of the current model and  $(-2\log \times \text{likelihood})$  of the saturated model.

Model	AICc	ΔAICc	w <sub>i</sub>	$\mathbf{L}$	K	D
P( <sub>MF#SG#PP</sub> , co)	582.89	0.00	0.10	1.00	7	568.67
P( <sub>MFF#SG#PP</sub> , co, si, bo)	583.37	0.48	0.08	0.79	9	565.01
P( <sub>MFF#SG#PP</sub> , co, si)	583.66	0.77	0.07	0.68	8	567.37
P( <sub>MFF#SG=PP</sub> , co, si, bo)	583.73	0.83	0.06	0.66	8	567.43
P( <sub>MF#SGG=PP</sub> , co)	583.81	0.91	0.06	0.63	6	571.64
P( <sub>MF#SGG=PP</sub> , co, si)	583.90	1.01	0.06	0.60	7	569.68
P( <sub>MF#SG#PPPP</sub> , ob, co, bo)	584.06	1.16	0.05	0.56	9	565.69
P( <sub>MF#SG#PPPP</sub> , ob, co)	584.13	1.23	0.05	0.54	8	567.84
$P(_{MF\#SG=PP}, co, bo)$	584.38	1.48	0.05	0.48	7	570.15
P( <sub>MF#SG#PP</sub> , ob, co, si, bo)	584.62	1.72	0.04	0.42	10	564.17
$P(_{MF=SG\#PP}, co, bo)$	584.89	2.00	0.04	0.37	7	570.67
P( <sub>MF#SG#PP</sub> , ob, co, si)	584.90	2.01	0.04	0.37	9	566.54
$P(_{MF=SG\#PP}, co, si)$	584.95	2.06	0.03	0.36	7	570.72
P( <sub>MF#SG=PP</sub> , ob, co, si, bo)	584.96	2.07	0.03	0.36	9	566.60
$P(_{MF\#SG=PP}, ob, co)$	585.03	2.14	0.03	0.34	7	570.81
P( <sub>MF#SG=PP</sub> , ob, co, si)	585.13	2.24	0.03	0.33	8	568.84
$P(_{MF=SG\#PP}, ob, co)$	585.19	2.29	0.03	0.32	7	570.96
P( <sub>MF=SG#PP</sub> , co, si, bo)	585.58	2.69	0.03	0.26	8	569.29
P( <sub>MF#SG=PP</sub> , ob, co, bo)	585.61	2.71	0.03	0.26	8	569.32
$P(_{MF=SG\#PP}, ob, co, bo)$	586.13	3.24	0.02	0.20	8	569.84
P( <sub>MF=SG#PP</sub> , ob, co, si)	586.19	3.29	0.02	0.19	8	569.90
P( <sub>MF=SG#PP</sub> , ob, co, si, bo)	586.83	3.93	0.01	0.14	9	568.46
$P(_{MF\#SG\#PP}, +t, co, bo)$	588.87	5.97	0.00	0.05	13	562.13
$P(_{MF\#SG\#PP}, +t, co)$	588.93	6.04	0.00	0.05	12	564.30

Model	AICc	<b>AAIC</b> c	Wi	L	K	D
P( <sub>MF#SG#PP</sub> , +t, co, si, bo)	589.46	6.57	0.00	0.04	14	560.60
$P(_{MF\#SG\#PP}, +t, co, si)$	589.73	6.83	0.00	0.03	13	562.98
P( <sub>MF#SG=PP</sub> , +t, co, si, bo)	589.79	6.90	0.00	0.03	13	563.05
$P(_{MF\#SG=PP}, +t, co)$	589.82	6.92	0.00	0.03	11	567.28
$P(_{MF\#SG=PP}, +t, co, si)$	589.94	7.04	0.00	0.03	12	565.30
$P(_{MF=SG\#PP}, +t, co)$	590.01	7.12	0.00	0.03	11	567.47
$P(_{MF=SG\#PP}, co)$	590.19	7.30	0.00	0.03	6	578.02
$P(_{MF\#SG=PP}, +t, co, bo)$	590.41	7.52	0.00	0.02	12	565.78
$P(_{MF=SG\#PP}, +t, co, bo)$	590.98	8.08	0.00	0.02	12	566.34
$P(_{MF=SG\#PP}, +t, co, si)$	591.03	8.13	0.00	0.02	12	566.39
$P(_{MF=SG=PP}, co)$	591.26	8.37	0.00	0.02	5	581.14
$P(_{MF=SG\#PP}, +t, co, si, bo)$	591.69	8.79	0.00	0.01	13	564.94
$P(_{MF=SG=PP}, ob, co)$	592.50	9.60	0.00	0.01	6	580.33
$P(_{MF=SG=PP}, co, si)$	592.55	9.66	0.00	0.01	6	580.38
$P(_{MF=SG=PP}, co, bo)$	593.17	10.27	0.00	0.01	6	581.00
P( <sub>MF=SG=PP</sub> , ob, co, si)	593.79	10.90	0.00	0.00	7	579.56
P( <sub>MF=SG=PP</sub> , ob, co, bo)	594.41	11.52	0.00	0.00	7	580.18
$P(_{MF=SG=PP}, co, si, bo)$	594.50	11.61	0.00	0.00	7	580.27
P( <sub>MF=SG=PP</sub> , ob, co, si, bo)	595.75	12.85	0.00	0.00	8	579.46
$P(_{MF\#SG=PP}, *t, co)$	595.99	13.09	0.00	0.00	21	552.07
$P(_{MF\#SG=PP}, *t, co, si, bo)$	596.24	13.34	0.00	0.00	23	547.94
$P(_{MF\#SG=PP}, *t, co, si)$	596.61	13.72	0.00	0.00	22	550.51
$P(_{MF=SG=PP}, +t, co)$	597.32	14.43	0.00	0.00	10	576.88
$P(_{MF\#SG\#PP}, *t, co)$	597.52	14.63	0.00	0.00	22	551.42
P( <sub>MF#SG#PP</sub> , co, bo)	597.94	15.05	0.00	0.00	8	581.65
$P(_{MF\#SG\#PP}, *t, co, si)$	598.29	15.40	0.00	0.00	23	549.99
$P(_{MF=SG=PP}, +t, co, si)$	598.62	15.73	0.00	0.00	11	576.09
$P(_{MF=SG=PP}, +t, co, bo)$	599.26	16.36	0.00	0.00	11	576.72
$P(_{MF=SG=PP})$	599.50	16.60	0.00	0.00	3	593.45
$P(_{MF=SG\#PP}, *t, co)$	599.79	16.90	0.00	0.00	21	555.88
$P(_{MF=SG=PP}, bo)$	600.41	17.51	0.00	0.00	4	592.33
$P(_{MF=SG\#PP}, *t, co, bo)$	600.56	17.66	0.00	0.00	22	554.45
$P(_{MF=SG=PP}, +t, co, si, bo)$	600.61	17.72	0.00	0.00	12	575.98
$P(_{MF=SG=PP}, ob)$	600.67	17.78	0.00	0.00	4	592.59
P( <sub>MF#SG=PP</sub> )	600.68	17.79	0.00	0.00	4	592.60
P( <sub>MF=SG#PP</sub> )	600.78	17.88	0.00	0.00	4	592.70
$P(_{MF=SG\#PP}, *t, co, si)$	600.87	17.97	0.00	0.00	22	554.76
$P(_{MF=SG\#PP}, *t, co, si, bo)$	601.12	18.22	0.00	0.00	23	552.82
P( <sub>MF=SG=PP</sub> , ob, bo)	601.59	18.70	0.00	0.00	5	591.47
P( <sub>MF=SG=PP</sub> , si)	601.78	18.88	0.00	0.00	4	593.70
P( <sub>MF#SG=PP</sub> , ob)	601.87	18.97	0.00	0.00	5	591.75

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Model	AICc	<b>∆AICc</b>	Wi	L	K	D
P( <sub>MF=SG#PP</sub> , ob)	601.96	19.07	0.00	0.00	5	591.84
P( <sub>MF=SG#PP</sub> , bo)	602.21	19.32	0.00	0.00	5	592.09
$P(_{MF=SG=PP}, *t, co)$	602.49	19.60	0.00	0.00	20	560.75
P( <sub>MF#SG#PP</sub> )	602.60	19.70	0.00	0.00	5	592.47
P( <sub>MF#SG=PP</sub> , ob, bo)	602.81	19.91	0.00	0.00	6	590.64
P( <sub>MF#SG=PP</sub> , si)	602.95	20.05	0.00	0.00	5	592.83
P( <sub>MF=SG=PP</sub> , ob, si)	602.98	20.08	0.00	0.00	5	592.85
P( <sub>MF#SG=PP</sub> , bo)	603.30	20.41	0.00	0.00	5	593.18
P( <sub>MF=SG#PP</sub> , ob, bo)	603.40	20.51	0.00	0.00	6	591.23
P( <sub>MF#SG#PP</sub> , bo)	603.65	20.76	0.00	0.00	6	591.48
P( <sub>MF=SG=PP</sub> , *t, co, si)	603.70	20.81	0.00	0.00	21	559.79
P( <sub>MF#SG#PP</sub> , ob)	603.79	20.89	0.00	0.00	6	591.62
P( <sub>MF=SG=PP</sub> , si, bo)	603.79	20.90	0.00	0.00	5	593.67
P( <sub>MF=SG#PP</sub> , si)	603.80	20.90	0.00	0.00	5	593.68
$P(_{MF=SG=PP}, *t, co, bo)$	604.00	21.11	0.00	0.00	21	560.09
P( <sub>MF#SG=PP</sub> , ob, si)	604.15	21.26	0.00	0.00	6	591.98
P( <sub>MF#SG#PP</sub> , si)	604.44	21.55	0.00	0.00	6	592.27
P( <sub>MF=SG=PP</sub> , *t, co, si, bo)	604.84	21.95	0.00	0.00	22	558.74
P( <sub>MF#SG#PP</sub> , ob, bo)	604.85	21.96	0.00	0.00	7	590.62
P( <sub>MF#SG=PP</sub> , si, bo)	604.91	22.01	0.00	0.00	6	592.74
P( <sub>MF=SG=PP</sub> , ob, si, bo)	605.00	22.10	0.00	0.00	6	592.83
P( <sub>MF=SG#PP</sub> , ob, si)	605.00	22.11	0.00	0.00	6	592.83
$P(_{MF=SG=PP}, +t)$	605.24	22.34	0.00	0.00	8	588.95
P( <sub>MF#SG#PP</sub> , ob, si)	605.65	22.76	0.00	0.00	7	591.43
P( <sub>MF=SG#PP</sub> , si, bo)	605.83	22.93	0.00	0.00	6	593.66
P( <sub>MF#SG=PP</sub> , ob, si, bo)	606.12	23.22	0.00	0.00	7	591.89
$P(_{MF=SG=PP}, +t, bo)$	606.18	23.29	0.00	0.00	9	587.82
P(MF#SG#PP, si, bo)	606.40	23.51	0.00	0.00	7	592.18
$P(_{MF\#SG=PP}, +t)$	606.47	23.58	0.00	0.00	9	588.11
$P(_{MF=SG\#PP}, +t)$	606.56	23.66	0.00	0.00	9	588.19
P( <sub>MF=SG#PP</sub> , ob, si, bo)	607.04	24.14	0.00	0.00	7	592.81
$P(_{MF\#SG=PP}, +t, bo)$	607.43	24.54	0.00	0.00	10	586.99
P( <sub>MF#SG#PP</sub> , ob, si, bo)	607.62	24.73	0.00	0.00	8	591.33
$P(_{MF=SG=PP}, +t, si)$	607.63	24.74	0.00	0.00	9	589.27
$P(_{MF=SG\#PP}, +t, bo)$	608.03	25.13	0.00	0.00	10	587.58
$P(_{MF\#SG\#PP}, +t)$	608.42	25.53	0.00	0.00	10	587.98
$P(_{MF\#SG=PP}, +t, si)$	608.84	25.94	0.00	0.00	10	588.39
$P(_{MF\#SG\#PP}, +t, bo)$	609.51	26.62	0.00	0.00	11	586.98
$P(_{MF=SG\#PP}, +t, si)$	609.69	26.80	0.00	0.00	10	589.24
P( <sub>MF=SG=PP</sub> , +t, si, bo)	609.69	26.80	0.00	0.00	10	589.24
$P(_{MF\#SG\#PP}, +t, si)$	610.37	27.48	0.00	0.00	11	587.84

Model	AICc	∆AICc	Wi	L	K	D
P( <sub>MF#SG=PP</sub> , +t, si, bo)	610.84	27.94	0.00	0.00	11	588.30
P( <sub>MF#SG=PP</sub> , *t, co, bo)	611.50	28.61	0.00	0.00	22	565.40
$P(_{MF\#SG\#PP}, *t, co, bo)$	611.53	28.63	0.00	0.00	23	563.23
$P(_{MF=SG\#PP}, +t, si, bo)$	611.76	28.87	0.00	0.00	11	589.22
$P(_{MF\#SG\#PP}, +t, si, bo)$	612.37	29.48	0.00	0.00	12	587.74
P( <sub>MF#SG#PP</sub> , *t, co, si, bo)	613.16	30.27	0.00	0.00	24	562.66
$P(_{MF=SG=PP}, *t)$	614.11	31.22	0.00	0.00	18	576.70
$P(_{MF\#SG=PP}, *t)$	614.37	31.47	0.00	0.00	19	574.80
$P(_{MF=SG\#PP}, *t)$	615.57	32.68	0.00	0.00	19	576.00
P( <sub>MF=SG=PP</sub> , *t, si, bo)	616.25	33.35	0.00	0.00	20	574.51
$P(_{MF\#SG\#PP}, *t)$	616.52	33.62	0.00	0.00	20	574.78
P( <sub>MF=SG=PP</sub> , *t, si)	616.59	33.70	0.00	0.00	19	577.02
P( <sub>MF#SG=PP</sub> , *t, si)	616.84	33.95	0.00	0.00	20	575.10
$P(_{MF\#SG=PP}, *t, bo)$	616.85	33.95	0.00	0.00	20	575.11
$P(_{MF=SG\#PP}, *t, bo)$	617.17	34.27	0.00	0.00	20	575.43
$P(_{MF\#SG\#PP}, *t, bo)$	617.56	34.67	0.00	0.00	21	573.65
P( <sub>MF=SG#PP</sub> , *t, si, bo)	618.36	35.46	0.00	0.00	21	574.44
$P(_{MF=SG=PP}, *t, bo)$	618.57	35.67	0.00	0.00	19	579.00
$P(_{MF=SG\#PP}, *t, si)$	618.60	35.71	0.00	0.00	20	576.86
P( <sub>MF#SG#PP</sub> , *t, si)	618.61	35.71	0.00	0.00	21	574.69
P( <sub>MF#SG=PP</sub> , *t, si, bo)	618.92	36.02	0.00	0.00	21	575.00
$P(_{MF\#SG\#PP}, *t, si, bo)$	620.69	37.80	0.00	0.00	22	574.59

Table 1.4. Model selection results for 128 models describing detection probabilities in three habitats (MF=mature forest, SG=Secondary growth forest, and PP=Pine plantation) and two observers (ob) for generalist species. Two mixtures were used with a common probability of inclusion ( $\pi$ ) in each mixture across habitat types. Detection probability was models as equal in the three habitats ( $P_{MF=SG=PP}$ ), as equal in the mature and secondary growth forests only (P<sub>MF=SG#PP</sub>), as equal in the secondary growth and pine plantations only (P<sub>MF#SG=PP</sub>), as different for all forest types (P<sub>MF#SG#PP</sub>). The covariates (bo=body length, co=regional commonness index, and si=singing propensity) were also used to model detection probability separately or in combination. In addition to habitat types and other covariates, I also modeled detection probabilities as a function of survey occasion (t) in an additive (+) and interactive (\*) way. Models are ranked by AICc.  $\Delta AIC_c$  is the difference in AIC<sub>c</sub> units from the highest ranking model. AIC<sub>c</sub> weights ( $w_i$ ), model likelihood (L), number of parameters (K), and deviance (D) are also shown. AICc weights sum to one and models with higher likelihood have more weight. Model likelihood is the likelihood of a model relative to the other models. Deviance is the difference in  $(-2\log \times \text{likelihood})$  of the current model and  $(-2\log \times \text{likelihood})$  of the saturated model.

Model	AICc	ΔAICc	w <sub>i</sub>	L	K	D
P(MF#SG#PP, ob, co, si, bo)	608.26	0.00	0.51	1.00	10	587.86
P( <sub>MF=SG#PP</sub> , ob, co, si, bo)	610.09	1.83	0.20	0.40	9	591.76
P( <sub>MF#SG#PP</sub> , co, si, bo)	611.96	3.70	0.08	0.16	9	593.63
P( <sub>MF#SG#PP</sub> , ob, co, si)	612.07	3.80	0.08	0.15	9	593.73
P( <sub>MF=SG#PP</sub> , ob, co, si)	613.31	5.05	0.04	0.08	8	597.05
P( <sub>MF=SG#PP</sub> , co, si, bo)	613.79	5.53	0.03	0.06	8	597.52
P( <sub>MF#SG#PP</sub> , +t, co, si, bo)	615.03	6.77	0.02	0.03	14	586.25
P( <sub>MF#SG#PP</sub> , co, si)	615.72	7.46	0.01	0.02	8	599.45
P( <sub>MF=SG#PP</sub> , +t, co, si, bo)	616.83	8.56	0.01	0.01	13	590.15
P( <sub>MF=SG#PP</sub> , co, si)	616.97	8.70	0.01	0.01	7	602.76
P( <sub>MF#SG#PP</sub> , +t, co, si)	618.82	10.56	0.00	0.01	13	592.14
P( <sub>MF#SG=PP</sub> , ob, co, si)	618.96	10.69	0.00	0.00	8	602.69
P( <sub>MF#SG=PP</sub> , ob, co, si, bo)	619.26	11.00	0.00	0.00	9	600.93
$P(_{MF=SG\#PP}, +t, co, si)$	620.03	11.77	0.00	0.00	12	595.45
P( <sub>MF#SG=PP</sub> , co, si, bo)	620.36	12.10	0.00	0.00	8	604.09
P( <sub>MF#SG#PP</sub> , ob, co, bo)	620.93	12.66	0.00	0.00	9	602.59
P( <sub>MF#SG=PP</sub> , co, si)	622.60	14.34	0.00	0.00	7	608.39
P( <sub>MF#SG=PP</sub> , *t, co, si, bo)	623.09	14.83	0.00	0.00	23	575.00
P( <sub>MF=SG#PP</sub> , ob, co, bo)	623.23	14.97	0.00	0.00	8	606.96
P( <sub>MF#SG=PP</sub> , ob, co, bo)	623.58	15.32	0.00	0.00	8	607.32
P( <sub>MF#SG#PP</sub> , ob, co)	624.37	16.11	0.00	0.00	8	608.11
P( <sub>MF#SG=PP</sub> , ob, co)	624.49	16.23	0.00	0.00	7	610.29
P( <sub>MF#SG#PP</sub> , co, bo)	624.60	16.33	0.00	0.00	8	608.33
P( <sub>MF#SG#PP</sub> , *t, co, si, bo)	624.62	16.36	0.00	0.00	24	574.34

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Model	AICc	<b>∆AICc</b>	Wi	L	K	D
P( <sub>MF=SG#PP</sub> , ob, co)	624.68	16.42	0.00	0.00	7	610.48
P( <sub>MF#SG=PP</sub> , +t, co, si)	625.68	17.42	0.00	0.00	12	601.10
$P(_{MF=SG\#PP}, *t, co, si, bo)$	625.99	17.72	0.00	0.00	23	577.90
$P(_{MF\#SG=PP}, +t, co, si, bo)$	626.02	17.76	0.00	0.00	13	599.34
$P(_{MF=SG=PP}, ob, co, si)$	626.28	18.02	0.00	0.00	7	612.07
P( <sub>MF=SG=PP</sub> , *t, co, si, bo)	626.39	18.13	0.00	0.00	22	580.48
P( <sub>MF#SG=PP</sub> , *t, co, si)	626.51	18.25	0.00	0.00	22	580.60
$P(_{MF=SG\#PP}, co, bo)$	626.86	18.60	0.00	0.00	7	612.66
P( <sub>MF=SG=PP</sub> , ob, co, si, bo)	627.08	18.82	0.00	0.00	8	610.82
P( <sub>MF#SG=PP</sub> , co, bo)	627.23	18.97	0.00	0.00	7	613.03
$P(_{MF=SG=PP}, ob, co)$	627.41	19.15	0.00	0.00	6	615.25
$P(_{MF\#SG\#PP}, +t, co, bo)$	627.68	19.41	0.00	0.00	13	601.00
$P(_{MF\#SG\#PP}, co)$	627.98	19.71	0.00	0.00	7	613.77
$P(_{MF\#SG=PP}, co)$	628.11	19.85	0.00	0.00	6	615.95
$P(_{MF=SG\#PP}, co)$	628.31	20.05	0.00	0.00	6	616.15
$P(_{MF\#SG\#PP}, *t, co, si)$	628.45	20.19	0.00	0.00	23	580.36
$P(_{MF=SG=PP}, ob, co, bo)$	628.75	20.48	0.00	0.00	7	614.54
$P(_{MF=SG=PP}, *t, co, si)$	628.80	20.53	0.00	0.00	21	585.05
P( <sub>MF#SG#PP</sub> , ob, si, bo)	629.38	21.12	0.00	0.00	8	613.11
$P(_{MF=SG\#PP}, *t, co, si)$	629.51	21.25	0.00	0.00	22	583.60
P( <sub>MF=SG=PP</sub> , co, si)	629.88	21.62	0.00	0.00	6	617.73
$P(_{MF=SG\#PP}, +t, co, bo)$	629.95	21.69	0.00	0.00	12	605.37
$P(_{MF\#SG=PP}, +t, co, bo)$	630.31	22.04	0.00	0.00	12	605.73
P( <sub>MF=SG=PP</sub> , co, si, bo)	630.70	22.44	0.00	0.00	7	616.50
$P(_{MF=SG=PP}, co)$	630.99	22.73	0.00	0.00	5	620.88
$P(_{MF\#SG\#PP}, +t, co)$	631.10	22.84	0.00	0.00	12	606.52
$P(_{MF\#SG=PP}, +t, co)$	631.19	22.93	0.00	0.00	11	608.70
$P(_{MF=SG\#PP}, +t, co)$	631.38	23.12	0.00	0.00	11	608.89
P( <sub>MF=SG#PP</sub> , ob, si, bo)	631.91	23.65	0.00	0.00	7	617.70
P( <sub>MF#SG=PP</sub> , ob, si, bo)	632.20	23.94	0.00	0.00	7	617.99
$P(_{MF=SG=PP}, co, bo)$	632.33	24.07	0.00	0.00	6	620.18
P( <sub>MF#SG#PP</sub> , si, bo)	632.81	24.55	0.00	0.00	7	618.61
$P(_{MF=SG=PP}, +t, co, si)$	632.97	24.71	0.00	0.00	11	610.49
P( <sub>MF=SG=PP</sub> , +t, co, si, bo)	633.81	25.54	0.00	0.00	12	609.23
$P(_{MF=SG=PP}, +t, co)$	634.08	25.82	0.00	0.00	10	613.68
P( <sub>MF#SG=PP</sub> , *t, co, bo)	635.01	26.74	0.00	0.00	22	589.09
P( <sub>MF=SG#PP</sub> , si, bo)	635.35	27.08	0.00	0.00	6	623.19
$P(_{MF=SG=PP}, +t, co, bo)$	635.45	27.19	0.00	0.00	11	612.96
P( <sub>MF#SG=PP</sub> , si, bo)	635.61	27.35	0.00	0.00	6	623.46
P( <sub>MF#SG#PP</sub> , +t, si, bo)	636.15	27.89	0.00	0.00	12	611.57
$P(_{MF=SG\#PP}, ob)$	636.37	28.11	0.00	0.00	5	626.26

Model	AICc	<b>∆AICc</b>	Wi	L	K	D
P( <sub>MF#SG#PP</sub> , *t, co, bo)	637.15	28.89	0.00	0.00	23	589.06
$P(_{MF=SG=PP}, *t, co, bo)$	637.97	29.71	0.00	0.00	21	594.23
$P(_{MF\#SG=PP}, *t, co)$	638.39	30.12	0.00	0.00	21	594.64
P( <sub>MF=SG#PP</sub> , +t, si, bo)	638.65	30.39	0.00	0.00	11	616.16
$P(_{MF\#SG=PP}, +t, si, bo)$	638.95	30.69	0.00	0.00	11	616.46
$P(_{MF=SG=PP}, *t, co)$	639.02	30.76	0.00	0.00	20	597.44
$P(_{MF=SG\#PP}, *t, co, bo)$	639.08	30.81	0.00	0.00	22	593.16
P( <sub>MF#SG#PP</sub> , ob)	639.89	31.62	0.00	0.00	6	627.73
P( <sub>MF=SG#PP</sub> )	639.95	31.69	0.00	0.00	4	631.88
P( <sub>MF#SG#PP</sub> , *t, co)	640.52	32.26	0.00	0.00	22	594.61
P( <sub>MF=SG#PP</sub> , *t, co)	641.03	32.77	0.00	0.00	21	597.28
P( <sub>MF#SG#PP</sub> , ob, bo)	641.58	33.31	0.00	0.00	7	627.37
P( <sub>MF=SG#PP</sub> , bo)	641.96	33.70	0.00	0.00	5	631.85
P( <sub>MF#SG=PP</sub> , ob, si)	642.35	34.08	0.00	0.00	6	630.19
$P(_{MF=SG\#PP}, +t)$	643.04	34.78	0.00	0.00	9	624.71
P( <sub>MF#SG#PP</sub> )	643.47	35.20	0.00	0.00	5	633.36
P( <sub>MF#SG=PP</sub> , *t, si, bo)	644.06	35.80	0.00	0.00	21	600.31
P(MF#SG#PP, ob, si)	644.23	35.97	0.00	0.00	7	630.02
P( <sub>MF#SG=PP</sub> , ob, bo)	644.69	36.43	0.00	0.00	6	632.54
P( <sub>MF#SG#PP</sub> , bo)	645.20	36.93	0.00	0.00	6	633.04
P( <sub>MF#SG=PP</sub> , si)	645.81	37.55	0.00	0.00	5	635.70
P( <sub>MF=SG=PP</sub> , *t, si, bo)	645.88	37.62	0.00	0.00	20	604.30
P( <sub>MF#SG#PP</sub> , *t, si, bo)	646.20	37.94	0.00	0.00	22	600.29
P( <sub>MF=SG=PP</sub> , ob, bo)	646.30	38.04	0.00	0.00	5	636.19
$P(_{MF\#SG\#PP}, +t)$	646.57	38.31	0.00	0.00	10	626.16
P(MF=SG#PP, ob, si)	647.24	38.97	0.00	0.00	6	635.08
P( <sub>MF=SG#PP</sub> , *t, si, bo)	647.61	39.34	0.00	0.00	21	603.86
P( <sub>MF=SG=PP</sub> , ob, si, bo)	647.69	39.42	0.00	0.00	6	635.53
P(MF#SG#PP, si)	647.69	39.43	0.00	0.00	6	635.53
P( <sub>MF=SG=PP</sub> , ob)	647.88	39.61	0.00	0.00	4	639.80
$P(_{MF\#SG=PP}, ob)$	648.16	39.90	0.00	0.00	5	638.05
$P(_{MF\#SG\#PP}, +t, bo)$	648.28	40.02	0.00	0.00	11	625.79
P( <sub>MF=SG=PP</sub> , ob, si)	648.65	40.39	0.00	0.00	5	638.54
P( <sub>MF#SG=PP</sub> , +t, si)	649.06	40.80	0.00	0.00	10	628.66
P( <sub>MF=SG=PP</sub> , bo)	649.91	41.65	0.00	0.00	4	641.84
P( <sub>MF=SG#PP</sub> , si)	650.58	42.32	0.00	0.00	5	640.47
$P(_{MF\#SG\#PP}, +t, si)$	650.98	42.72	0.00	0.00	11	628.49
P( <sub>MF=SG=PP</sub> , si, bo)	651.05	42.79	0.00	0.00	5	640.94
P( <sub>MF#SG=PP</sub> , +t, bo)	651.38	43.12	0.00	0.00	10	630.98
P( <sub>MF=SG=PP</sub> )	651.47	43.21	0.00	0.00	3	645.42
$P(_{MF\#SG=PP})$	651.75	43.49	0.00	0.00	4	643.67

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Model	AICc	∆AICc	Wi	L	K	D
P( <sub>MF=SG=PP</sub> , si)	652.06	43.80	0.00	0.00	4	643.99
P( <sub>MF#SG=PP</sub> , bo)	652.50	44.24	0.00	0.00	5	642.39
$P(_{MF=SG\#PP}, *t)$	653.25	44.99	0.00	0.00	19	613.82
$P(_{MF=SG\#PP}, +t, si)$	653.97	45.71	0.00	0.00	10	633.56
$P(_{MF=SG=PP}, +t, si, bo)$	654.44	46.18	0.00	0.00	10	634.03
$P(_{MF=SG=PP}, +t)$	654.52	46.26	0.00	0.00	8	638.25
$P(_{MF=SG=PP}, +t, bo)$	654.61	46.34	0.00	0.00	9	636.27
$P(_{MF\#SG=PP}, +t)$	654.82	46.56	0.00	0.00	9	636.49
$P(_{MF=SG=PP}, +t, si)$	655.36	47.10	0.00	0.00	9	637.03
$P(_{MF\#SG\#PP}, *t)$	655.49	47.22	0.00	0.00	20	613.90
P( <sub>MF=SG#PP</sub> , ob, bo)	655.77	47.51	0.00	0.00	6	643.62
$P(_{MF\#SG\#PP}, *t, bo)$	657.42	49.15	0.00	0.00	21	613.67
P( <sub>MF#SG=PP</sub> , *t, si)	659.49	51.23	0.00	0.00	20	617.91
P( <sub>MF#SG#PP</sub> , *t, si)	661.09	52.83	0.00	0.00	21	617.35
$P(_{MF=SG\#PP}, +t, bo)$	662.51	54.25	0.00	0.00	10	642.11
$P(_{MF\#SG=PP}, *t, bo)$	662.80	54.53	0.00	0.00	20	621.21
P( <sub>MF=SG=PP</sub> , *t, si)	663.18	54.92	0.00	0.00	19	623.75
P( <sub>MF=SG#PP</sub> , *t, si)	664.53	56.26	0.00	0.00	20	622.94
$P(_{MF=SG=PP}, *t)$	665.72	57.46	0.00	0.00	18	628.44
P( <sub>MF#SG=PP</sub> , *t)	666.03	57.77	0.00	0.00	19	626.60
$P(_{MF=SG=PP}, *t, bo)$	666.33	58.06	0.00	0.00	19	626.90
$P(_{MF=SG\#PP}, *t, bo)$	672.86	64.60	0.00	0.00	20	631.28



Figure 1.1. Model-averaged detection probability for the first occasion in different habitat types (MF=mature forest, SG=secondary growth forest, and PP=pine plantation) for the total species richness analysis. 95% confidence intervals are shown; the probability of being in mixture 1 is 0.26 (95% CI = 0.18, 0.35). Species with high detection probabilities were categorized in mixture 1 and species with low detection probabilities are categorized in mixture 2.



Figure 1.2. Model-averaged detection probability of species with high and low singing propensity during the first occasion for the mixture of higher detection probability in mature forest for the total species richness analysis. 95% confidence intervals are shown.



Figure 1.3. Model-averaged species richness estimates for mature forest, secondary forest and pine plantations. 95% confidence intervals are shown.



Figure 1.4. Model-averaged detection probabilities for the first occasion in different habitat types (MF=mature forest, SG=secondary growth forest, and PP=pine plantation) for specialist species. 95% confidence intervals are shown; the probability of being in mixture 1 is 0.31 (95% CI = 0.18, 0.47). Species with high detection probabilities were categorized in mixture 1 and species with low detection probabilities are categorized in mixture 2.



Figure 1.5. Model-averaged detection probability of species with high and low singing propensity during the first occasion for the mixture of higher detection probability in mature forest for the forest specialist species. 95% confidence intervals are shown.



Figure 1.6. Model-averaged detection probability for the first occasion in different habitat types (MF=mature forest, SG=secondary growth forest, and PP=pine plantation) for generalist species. 95% confidence intervals are shown; the probability of being in mixture 1 is 0.26 (95% CI = 0.15, 0.41). Species with high detection probabilities were categorized in mixture 1 and species with low detection probabilities are categorized in mixture 2.



Figure 1.7. Model-averaged detection probability of species with high and low singing propensity during the first occasion for the mixture of higher detection probability in mature forest for the forest generalist species. 95% confidence intervals are shown.

# **CHAPTER 2**

# ROAD CROSSING BY BIRDS IN A TROPICAL FOREST IN NORTHERN VIETNAM

Abstract: Gaps, such as those caused by roads and powerlines, have been shown to have adverse effects on wildlife in general, and birds in particular, in forested landscapes. In addition to other effects, gaps may serve as a barrier to movement in continuous forest. Roads may serve as linear, inhospitable gaps that inhibit movement. Studies on gap-crossing have been conducted worldwide, and many forest bird species have been shown to be reluctant to cross gaps. Few studies, however, have been conducted to demonstrate whether birds perceive roads as gaps and how bird movement is affected by such narrow linear gaps. No such studies have been conducted in tropical Southeast Asia. My study examined whether forest birds in Southeast Asia are inhibited from crossing roads by using a territorial call playback. Specifically, I compared bird movement over a paved road (6-8m wide) within forest interior plots in Cuc Phuong National Park, northern Vietnam in summer 2007. I focused on four species in the Sylviidae family: Striped Tit Babbler (Macronous gularis), Rufous-throated Fulvetta (Alcippe danisi), Puff-throated Babbler (Pellorneum ruficeps), and Buff-breasted Babbler (Pellorneum tickelli). I grouped species by foraging height: Striped Tit Babbler and Rufous-throated Fulvetta forage in the mid-canopy while Puff-throated Babbler and Buff-

breasted Babbler feed on the ground. The probabilities of approaching the playback were higher for mid-canopy species than for the ground species. The probabilities of approaching the playback for mid-canopy species at the road sites (0.92; 95% CI = 0.84,0.97 for Striped Tit Babbler and 0.88, 95% CI = 0.78, 0.94 for Rufous-throated Babbler) were similar to those in forest interior (0.96; 95% CI = 0.88, 0.98 for Striped Tit Babbler)and 0.93; 95% CI = 0.84, 0.97 for Rufous-throated Fulvetta). The probabilities of approaching the playback for ground species at the road site (0.77; 95% CI = 0.66, 0.86)for Puff-throated Babbler and 0.69; 95% CI = 0.57, 0.78 for Buff-breasted Babbler) were lower than those in the forest interior (0.85; 95% CI = 0.73, 0.92 for Puff-throated)Babbler and 0.82; 95% CI = 0.72, 0.89 for Buff-breasted Babbler). The response delay time of the mid-canopy group was less than the response delay time of the ground species. The response delay time for all species at the road sites (2.39 minutes; 95% CI =1.85, 2.92 for Striped Tit Babbler, 2.50; 95% CI = 1.96, 3.04 for Rufous-throated Babbler, 3.27 minutes; 95% CI = 2.75, 3.79 for Puff-throated Babbler, and 3.23 minutes; 95% CI = 2.72, 3.75 for Buff-breasted Babbler) were slightly less than those in forest interior (2.11; 95% CI = 1.69, 2.52 for Striped Tit Babbler, 2.22; 95% CI = 1.74, 2.70 for Rufous-throated Fulvetta, 3.10; 95% CI = 2.60, 3.54 for Puff-throated Babbler, and 3.03minutes; 95% CI = 2.60, 3.47 for Buff-breasted Babbler). The road seems to moderately affect the ability for ground-feeding species birds to cross gaps and not affect species that live mostly in the mid-canopy and high canopy. In the course of economic development, many more gaps in general, and roads in particular, will be imposed on the forest landscapes. These roads, especially in the natural reserves, should be designed to be as narrow as possible, and to keep the forest canopy over the gaps as closed as possible. In

the areas where ground birds are of interest or endangered, road construction should be avoided.
## **INTRODUCTION**

Roads have been shown to have adverse effects on wildlife in general, and birds in particular, in forested landscapes (Forman and Alexander 1998, Laurance et al. 2004). Roads can cause increased forest fragmentation, changes in plant composition, increased noise, and higher levels of exotic invasions by plant and wildlife species (Reijnen et al. 1995). These effects can lead to changes in bird community composition and population density of some species (Reijnen et al. 1995). Some species may be attracted to habitats near roads because of heterogeneous vegetation, but ultimately animals inhabiting these environments have lower survival and/or reproduction such that roads may cause such habitats to become ecological traps (Schlaepfer et al. 2002), especially if animals die crossing roads (Mech 1989, Savidge et al. 1992, Forman and Alexander 1998).

Roads may also serve as a behavioral barrier to bird movement (Develey and Stouffer 2001, Dyer et al. 2002). In continuous forest, roads may serve as a linear, inhospitable gap that inhibits birds from moving across the road. Studies on gap-crossing have been conducted worldwide, and many forest bird species have been shown to be reluctant to cross gaps (Sieving et al. 1996, Desrochers and Hannon 1997, Grubb and Doherty 1999, Belisle and Desrochers 2002, Creegan and Osborne 2005, Laurance 2005). One possible reason many song birds avoid such open areas is that the predation risk, mostly from raptors (Desrochers and Hannon 1997), is thought to be higher in these areas.

Few studies have been conducted to demonstrate whether birds perceive roads as gaps and how bird movement is affected by such narrow linear gaps (Develey and Stouffer 2001, Laurance et al. 2004). No such studies have been conducted in tropical

Southeast Asia. Understanding gap crossing ability in birds in Southeast Asia is important because this region supports a large area of tropical forest rich in bird species, has been identified as a conservation area of concern, especially for birds (Sodhi and Brook 2006), and is experiencing a high degree of economic development. This economic development leads to increased road and power line construction as well as an increased need for protecting wildlife in these areas. How such roads and power line corridors affect bird movement has not been considered by wildlife managers in this part of the world and this information will be useful to land planners in the face of rapid urbanization.

My study examined whether forest birds in Southeast Asia are inhibited from crossing roads by using a territorial call playback. Specifically, I compared bird movement over a paved road (6-8m wide) within forest interior plots. I tested two predictions: (1) birds are not as willing to cross roads to investigate audio playback sources as they are in forest interior; and (2) when birds do respond to audio playback, the duration from the start of playback call to bird's approaching playback will be longer at road sites as compared to the forest interior.

#### **METHODS**

## Study area

The research was conducted in Cuc Phuong National Park (CPNP), Vietnam, located 100 km south of the capital, Hanoi ( $20^{\circ}$  14' –  $20^{\circ}$  24' N;  $105^{\circ}$  29' –  $105^{\circ}$  44' E; Appendix I). The park is 22,000 ha in size and located in three provinces: Ninh Binh, Hoa Binh, and Thanh Hoa. The park is mostly composed of typical limestone forest with the highest elevation being 700 m. Because the park has been well-protected, the forest remains essentially intact with canopy heights reaching 40-50 m.

The climate in CPNP is tropical with two distinctive seasons caused by monsoon winds. The hot and rainy season is from May to November while the cold and dry season is from December through April. The average year-round temperature is 20.6°C, the annual minimum temperature is 0.7°C, and the maximum temperature reaches 39°C. The park receives ~21 cm precipitation each year and relative humidity averages 90%.

My specific study site was located along a valley cutting through the park in North-South direction. A 20 km paved road which was established 15 years ago runs through the valley and was used as the road gap. The road is 6-8 m wide with a 5 m paved surface and is covered by forest canopy. The forest understory on both sides of the road is not disturbed. This road is used mainly for forest management and tourism with about 30 vehicles passing along the road per day. My reference areas were located in interior forest areas at least 200 m from the nearest road.

# **Study species**

I focused on four species in the Sylviidae family: Striped Tit Babbler (*Macronous gularis*), Rufous-throated Fulvetta (*Alcippe danisi*), Puff-throated Babbler (*Pellorneum ruficeps*), and Buff-breasted Babbler (*Pellorneum tickelli*). In natural forest, these species are abundant, generating a large sample size for the study. Striped Tit Babblers weigh from 10-12g (Vu, unpublished), live in small flocks and are usually found in mid-canopy. Rufous-throated Fulvettas weigh from 16-18g, live in small flocks and are usually found in understory to mid-canopy in old growth forest. Puff-throated Babblers

and Buff-breasted Babblers have body masses from 26-28g and 16-18g, respectively. These two species live solitarily or in pairs and are usually found feeding on the ground or in the understory layer.

#### **Gap-crossing trials**

Data were collected from May to August, 2007. Trials were conducted from 6h00 to 10h00 in the morning and from 3h00 to 6h00 in the afternoon when the birds are most active. Data were only collected during favorable weather conditions (e.g. the trials were not conducted in rainy and windy weather). I used a playback of a territorial call of the targeted species to elicit directional movement of birds as has been used in previous studies (Sieving et al. 1996, Develey and Stouffer 2001, Harris and Reed 2001). Calls were obtained from Scharringa (2005). Bird calls were played using a Sansa 150c Mp3 player and broadcasted using a directional SME-AFS Amplified Playback Field Speaker System.

At the road sites, three people walked along the road detecting birds. When a bird was detected, one person entered 5m into the forest on the opposite side of the road from the target bird and played the audio tape until the bird crossed the road, or for a maximum of 10 minutes. Two other people hid in locations where they could track and record the movement of the focal bird. At the reference site (forest interior), the procedures were the same as for the road sites at similar distances from a focal bird. A positive response was defined as a bird crossing the road to approach the playback call. For the forest trials, a positive response was recorded when the target bird came within 5 m of the playback set up. For species that live in flocks, the flocks were treated as the sampling

unit and trials were terminated once the first bird in the flock was observed to approach the playback source closely.

The duration from the beginning of the playback until the bird crossed the road was determined and referred to as the response delay time. All trials were conducted at least 200 m from each other to assure independence of birds. This distance was chosen from published studies on avian home ranges of small understory birds in tropical forest, such as the species targeted (Jansen 1999, Dale and Slembe 2005). However, in 59 cases, two birds were clearly distinguished as being separate by observers but were less than 200 m (minimum 50 m) and playback trials were conducted. I used a directional amplifier to transmit the playback calls, therefore, nearby non-target birds were not likely to hear the calls.

Several studies have shown that the probability of success of territorial playback calls in attracting birds is close to one in the forest interior (Sieving et al. 1996, Develey and Stouffer 2001). An earlier pilot study also indicated a high propensity for birds to approach my playback in the forest interior. Using information from the pilot study, I calculated the necessary sample size (Zar 1998). I set power and significance level to 80% and 0.05, respectively. The sample size sufficient to detect an effect size of 20% was 48 for my "treatment" (road) and reference (forest interior) groups.

## **Data Analysis**

Data on the percentage of positive responses out of total trials were analyzed using Proc LOGISTIC (SAS v.9.00, SAS 2002). I constructed 8 models including models with no effect, three single main effect models (road, foraging height (height),

and species) and models with additive and interactive combinations of 'road' with 'height,' and 'road' with 'species'. I grouped species by foraging height. Striped Tit Babbler and Rufous-throated Fulvetta forage in the mid-canopy and were grouped together, while Puff-throated Babbler and Buff-breasted Babbler which feed on the ground, were grouped together. Due to complete dependence between species and foraging height covariates, the models containing both species and foraging height were not constructed. Akaike's Information Criteria (AICc) was used for model selection in investigating the factors that influence the response delay time. Additionally, AICc weights (w), cumulative AICc weights  $(w_i)$  and parameter estimates were used to assess the models (Burnham and Anderson 2002). However, the number of times 'road' factor appears in the models (five times) was higher than 'foraging height' and 'species' covariates (three times); therefore, to examine the relative importance of the road factor to other covariates, an adjusted cumulative AICc weight  $(3/5 \text{ of } w_i)$  for the road was used. Parameters of interest were model-averaged across the entire model set if multiple models had non-trivial AICc weights (Burnham and Anderson 2002).

For trials in which birds responded, data on the duration from the start of playback call to bird's approaching playback were analyzed using Proc MIXED (SAS v.9.00, SAS 2002). I constructed 8 models including models with no effect, three single main effect models (road, foraging height (height), and species) and models with additive and interactive combinations between 'road' and 'height' and 'road' and 'species'. Due to complete dependence between species and foraging height covariates, the models containing both species and foraging height were not constructed. Akaike's Information Criteria (AICc) was used for model selection in investigating the factors that influence

the response delay time. Additionally, AICc weights (w), cumulative AICc weights ( $w_i$ ) and parameter estimates were used to assess the models (Burnham and Anderson 2002). However, the number of times the 'road' factor appear in the models (five times) was higher than 'foraging height' and 'species' covariates (three times), therefore, I used an adjusted cumulative AICc weight (3/5 of  $w_i$ ) for the road factor. Parameters of interest were model-averaged across the entire model set if multiple models had non-trivial AICc weights (Burnham and Anderson 2002).

## RESULTS

I conducted 46 and 81 independent trials along the road and in the forest interior for Striped Tit Babbler, respectively. Trials for Rufous-throated Fulvetta, Puff-throated Babbler, and Buff-breasted Babbler were 36 and 54, 42 and 38, and 46 and 77 for road and interior forest sites, respectively. All species responded strongly to the calls. Striped Tit Babblers were often detected in flocks of 2-5 individuals, Rufous-throated Fulvettas were often detected in flocks of 2-4 birds, and Puff-throated Babblers and Buff-breasted Babblers were often detected solitarily or in pairs. Most individuals were initially detected through their songs or calls.

No single model explained the probability of approaching the playback adequately (Table 2.1). A model in which probability of approaching the playback was influenced by an additive combination between road and species had the strongest support, with w = 0.36. The second best model which included an additive combination between road and foraging height also had high support (w = 0.27, and  $\Delta AICc = 0.62$ ; Table 2.1). Models containing additive effects of road and species plus an interactive term between road and species also had some support (w = 0.16, and  $\Delta AICc = 1.68$ ) as did a model containing additive effects of road and foraging height plus an interactive term between road and foraging height (w = 0.11, and  $\Delta AICc = 2.36$ ; Table 2.1). By examining the cumulative AICc weight ( $w_i$ ), there was evidence that variation in the probability of approaching the playback was influenced by foraging height ( $w_i = 0.57$ ), road (adjusted AICc weight  $w_i = 0.54$ ), and species ( $w_i = 0.43$ ; Table 2.1 and Fig. 2.1). The effect of road on the probability of approaching the playback varies by species and foraging height. The effect of road on bird movement was very small for the mid-canopy group including Striped Tit Babbler and Rufous-throated Fulvetta (Fig. 2.1). Groundfeeding species (Puff-throated Babbler and Buff-breasted Babbler) were more prone to be affected by the road. Buff-breasted Babbler was the species that showed greatest reduced probability of approaching the playback at the road (Fig. 2.1). A model in which the probability of approaching the playback was similar between road and forest or constant over species or foraging height received no weight and  $\Delta AICc = 19.38$  (Table 2.1).

For the trials in which the target individuals did respond, no single model explained variation in response delay time adequately. Models in which the response delay time was influenced by road and foraging height had the highest support (w = 0.33; Table 2.2). The second best model incorporated foraging height as the explanatory variable and had an AICc weight = 0.25 and  $\Delta$ AICc = 0.57. A model including road and foraging height and an interactive term of these two factor had some support (w = 0.18,  $\Delta$ AICc = 1.24). The model in which response delay time was influenced by road and species had AICc weight = 0.12 and  $\Delta$ AICc = 1.99. These results indicate that the response delay time was influenced mostly by foraging height (cumulative AICc weight

 $w_i = 0.76$ ) and some by the effect of road (adjusted cumulative AICc weight  $w_i = 0.39$ ). Species also had some support with a cumulative AICc weight = 0.24. The response delay time was higher in the ground-feeding group than in the canopy-foraging group (Fig. 2.2). The response delay time was slightly higher in the road site as compared to the forest interior (Fig. 2.2).

## DISCUSSION

Similar to other studies using territorial call playbacks to attract birds (Sieving et al. 1996, Develey and Stouffer 2001), the attraction of birds in my forest interior sites was very high. All species responded quickly to the playback and moved toward the playback source. When individuals were in proximity of the playback, their singing rate increased and they sang loudly. Most birds were initially detected through their songs or calls. Therefore, the results of my study are probably more representative of the behavior of territorial males because male birds generally sing and call more often then females do.

In both analyses, foraging height had the strongest influence on dependent variables and carried the highest cumulative AICc weight. Road was the second best variable explaining variation of probability of approaching the playback and response delay time. Mid-canopy foraging species, Striped Tit Babbler and Rufous-throated Fulvetta, responded more quickly and frequently than the other two ground-feeding species and this may be because they live in flocks and the aggressive response of a flock may be higher than that of individuals. Additionally, mid-canopy foraging species did not show a reduced propensity of approaching the playback at the road site as compared

to forest interior whereas ground-feeding species did. This can be explained partially by the better cover over the road at the mid-canopy height.

The delay response time was lower in the mid-canopy foraging group which was consistent with the higher probability of approaching the playbacks. The response delay times in forest interior sites were slightly lower than the road sites. This result was consistent with other observations, in which birds showed a slight hesitation as they approached the edge of the forest. This timidity might reflect anti-predator behavior or anti-risk behavior (Desrochers and Hannon 1997).

Several studies (Sieving et al. 1996, Harris and Reed 2001) have demonstrated that playback methods can be effective. Develey and Stouffer (2001) showed that the arrangement of roads on bird territories negatively and strongly affected the propensity for birds to cross more open roads but did not affect the propensity for birds to cross vegetation-covered roads. The road I studied in Cuc Phuong National Park had a closed canopy and little traffic: the risks associated with the road might have been low for the birds we studied. Because birds are likely to always respond to playbacks transmitted within their territories (McGregor and Horn 1992, Betts et al. 2005), the low effect of roads on bird movement in this study can be due to the fact that this road does not seem to function as a territory boundary for solitary or flocking birds. The road through Cuc Phuong may be suitable habitat with low predation rates and other risks (Desrochers and Hannon 1997, Clair 2003). The road has also been imposed on the landscape for a long time (20 years) so birds may have adapted to its presence.

In conclusion, tourism roads of the type that appear in Cuc Phuong National Park seem not to affect species that live mostly in the mid-canopy and high canopy because of

the relatively slight disturbance of the road to the canopy. Larger species than those targeted in this study may also be less affected (Grubb and Doherty 1999). The road seems to moderately affect the ability for ground-feeding species of birds to cross these gaps. In the course of economic development, many more gaps in general or roads in particular will be imposed on the forest landscapes. These roads, especially in natural reserves, should be designed to be as small as possible and to keep the forest canopy over the gaps as closed as possible. In the areas where ground birds are of interest or endangered, road construction should be avoided.

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Table 2.1. Model selection results for 8 models describing probability of approaching the playback source (Prob). Model set includes models with no effect (model with intercept only), three models with a single effect (road, foraging height (height), and species) and models with additive (+) and interactive combinations (\*) between 'road' and 'foraging height' and 'road' and 'species.' Models are ranked by AICc.  $\Delta$ AICc is the difference in AICc units from the highest ranking model. AICc weights ( $w_i$ ), model likelihood (L), - 2Loglikehood (-2LogL), number of parameters (K), and deviance (D) are also shown. Model likelihood is the likelihood of a model relative to the other models. AICc weights sum to one and models with higher likelihood have more weight. Deviance is the difference in (-2log × likelihood) of the current model and (-2log × likelihood) of the saturated model.

Model	AICc	ΔAICc	<i>w</i> <sub>i</sub>	L	-2LogL	K	D
Prob = Road + Species	334.21	0.00	0.36	1.00	324.07	5	4.53
Prob = Road + Height	334.84	0.62	0.27	0.73	328.78	3	9.24
Prob = Road + Species + Road*Species	335.89	1.68	0.16	0.43	319.54	8	0.00
Prob = Road + Height + Road*Height	336.58	2.36	0.11	0.31	328.48	4	8.94
Prob = Height	338.04	3.82	0.05	0.15	334.01	2	14.47
Prob = Species	338.15	3.93	0.05	0.14	330.05	4	10.51
Prob = Road	349.51	15.29	0.00	0.00	345.48	2	25.94
Prob = intercept only	353.60	19.38	0.00	0.00	351.59	1	32.05

Table 2.2. Model selection results for 8 models describing delay time before approaching the playback source. Model set includes models with no effect (model with intercept only), three models with a single effect (road, foraging height (height), and species) and models with additive (+) and interactive combination (\*) between 'road' and 'foraging height' and 'road' and 'species'. Models are ranked by AICc.  $\Delta$ AICc is the difference in AICc units from the highest ranking model. AICc weights ( $w_i$ ), model likelihood (L), -2Loglikehood (-2LogL), number of parameters (K), and deviance (D) are also shown. Model likelihood is the likelihood of a model relative to the other models. AICc weights sum to one and models with higher likelihood have more weight. Deviance is the difference in (-2log × likelihood) of the current model and (-2log × likelihood) of the saturated model.

Model	AICc	ΔAICc	Wi	L	-2LogL	K	D
Time = Road + Height	1596.06	0.00	0.33	1.00	1590.00	3	3.20
Time = Height	1596.63	0.57	0.25	0.75	1592.60	2	5.80
Time = Road + Height + Road*Height	1597.30	1.24	0.18	0.54	1589.20	4	2.40
Time = Road + Species	1598.04	1.99	0.12	0.37	1587.90	5	1.10
Time = Species	1598.30	2.24	0.11	0.33	1590.20	4	3.40
Time = Road + Species + Road*Species	1603.15	7.09	0.01	0.03	1586.80	8	0.00
Time = Road	1607.03	10.97	0.00	0.00	1603.00	2	16.20
Time = intercept only	1607.71	11.65	0.00	0.00	1605.70	1	18.90



Figure 2.1. Model-averaged probability of approaching playback calls by species and habitat types. 95% confidence intervals are shown.



Figure 2.2. Model-averaged response delay time (minutes) by species and habitat types. 95% confidence intervals are shown.

# **CHAPTER 3**

# EFFECT OF DIFFERENT LOGGING SCHEMES ON BIRD COMMUNITIES IN TROPICAL FORESTS: A SIMULATION STUDY

Abstract: Tropical forest ecosystems harbor the greatest biodiversity in the world and the extreme reduction of natural tropical forest cover worldwide is a current cause of concern. This pattern has been observed in the tropics of Asia, leading to the local extinction of many bird populations. Much of the remaining forest is also being changed to disturbed or second growth forests. Most of the tropical forests in Asia are located in developing countries. These countries heavily utilize their natural resources, such as tropical forests, for development such that setting aside remaining natural forests for conservation purposes is impossible. Balancing economic activities, such as logging, with conservation programs will play an important role in conserving the rich biodiversity in these regions. Therefore, the effects of logging on biodiversity needs to be understood more thoroughly. I modeled the recovery of avian communities following a variety of potential logging schemes that varied by the logging interval (1-100 years) and the wood volume left after harvesting (0-100%). Based on avian habitat requirements, I divided forest birds into two categories, forest specialist and forest generalist species. The recovery processes of these two groups of species associated with the forest succession gradient is different and leads to changes in avian communities.

The recovery rate of forest generalists is very high during the first 15 years of succession and then becomes asymptotic. The recovery rate of forest specialists remains high until about 50 years of succession. After 50 years, the recovery rate is lower, and fewer bird species colonize in subsequent years. Logging schemes with either a logging cycle > 15 years or wood volume left after harvesting > 30% resulted in 70% of the regional forest bird species pool being conserved. To conserve 80% of the species pool, logging schemes with either cycle length > 40 years or wood volume left after harvest > 55% should be implemented. My simulations provide a prediction of how avian communities could be affected under different logging schemes and can provide guidance to management agencies in developing tropical forested countries.

# **INTRODUCTION**

Tropical forests contain a greater level of biodiversity as compared to any other ecosystem in the world (Lewis 2009). The extreme reduction of natural tropical forest cover worldwide is a current cause of concern (Collar et al. 1994, Sodhi et al. 2004, Sodhi et al. 2008). This pattern has been observed in the tropics of Asia, leading to the local extinction of many bird populations (Sodhi and Brook 2006). Meanwhile, much of the remaining forest is still being degraded due to anthropogenic activities, and changed to disturbed or second growth forests. Most of the tropical forests in Asia are located in developing countries. These countries heavily utilize their natural resources, such as tropical forests, for development and setting aside all natural forests for preservation purposes is unrealistic. Therefore, balancing economic activities, such as logging, with conservation programs will play an important role in conserving the rich biodiversity in these regions.

Bird communities are strongly influenced by habitat change (Terborgh et al. 1990, Wiens 1992), and are sensitive to disturbances. However, few studies have focused on the impacts of logging on bird communities in the tropical forests, especially in Asia (Lambert 1992, Mason 1996, Dunn 2004a, Holbech 2005, Barlow et al. 2006). These empirical studies have been limited to short term effects of a few logging schemes and have not revealed the long term recovery of avian communities after forest disturbance. Kohler et al. (2002) conducted a modeling study on the effect of logging on birds in Asia, but the habitat was limited to dipterocarp forest and did not consider tropical evergreen forests (not to be confused with conifer forests such as those found in North America). Dipterocarp and evergreen tropical forests are both common, but contrast strongly with each other. Dipterocarp forests are deciduous, structurally simple, and are low in tree species diversity. In contrast, tropical evergreen forests are structurally complex and high in tree species diversity. Given the difference in vegetation, the fauna inhabiting these two types of forests differ as well. Therefore, Kohler et al.'s (2002) study cannot be used for inference to tropical evergreen forest ecosystems, but similar studies are needed to better understand how bird communities might recover from logging in the evergreen forests. In this chapter I address this informational need.

Based on habitat requirements, I divided forest bird species into two categories, forest specialist and forest generalist species. Forest specialist species are the species that mostly inhabit later succession stages while forest generalist species tend to inhabit all succession stages. The recovery process, along a forest succession gradient after logging, leads to changes in avian communities through time. The recovery process is likely to be different between these two types of species. Forest generalists may recover in early succession stages faster than forest specialist species and as the habitat approaches later succession stages, more forest specialist species will inhabit the forest. The objective of my study is to better understand the recovery process for avian communities under different logging schemes in tropical evergreen forests. My study simulated the effect of different logging schemes on tropical forest biodiversity, focusing on birds, and I provide recommendations concerning logging cycles (LC) and the amount of wood volume that should be left after logging events (WL).

# METHODS

# Forest growth model and logging schemes

I simulated forest growth and succession using MYRLIN (Alder et al. 2002) and using data by Steininger (2000). MYRLIN was developed to specifically model the growth of tropical evergreen forests. The pattern of diameter increment of tropical forest trees are similar among regions, allowing general assumptions to be made about growth rate and yield predictions (Alder et al. 2002, Vanclay 2003). The results from MYRLIN are used as guidelines for harvest regulation and forest management (Alder et al. 2002).

I ran the MYRLIN model to simulate forest growth per hectare up to 300 years after clearcut logging events. The MYRLIN model cannot provide predictions for areas smaller than 78  $m^3$ /ha, therefore, when needed, I estimated the volume of forest below 78  $m^{3}$ /ha using data by Steininger (2000). Three hundred years was chosen as an adequate time period for a tropical forest to recover to a climax stage. These simulation data were used to reset and track the age and volume of the forest after each logging event. I investigated the effects of 441 logging schemes on bird communities. These schemes were combinations of 21 logging rotation cycles (1, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 75, 80, 85, 90, 95, and 100 years) and 21 intensity levels in which 0, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 75, 80, 85, 90, 95, and 100 percent of the forest volume was left after logging events (with the baseline being the entire forest stand being at the 300 year old climax stage). Less wood volume left after logging events is equivalent to higher logging intensity. The growth of forest older than 100 years is very slow (Vu, pers. comm.), therefore; rotations longer than 100 years are not practical. In each logging scheme, only the largest size classes of trees were cut to mimic realistic forest logging practices.

# **Bird community dynamics**

Bird community dynamics were modeled using data from Raman (1998). This study was carried out in Mirozam, north-east India (23°20' to 23°20' N and 92°15' 23°30' E) along a tropical evergreen forest succession gradient. This region borders Southeast-Asia. Twelve transects in each forest age class type (1, 5, 10, 25, 100, 300 years after clearing) were surveyed 10 times between December 1994 and April 1995. Numbers of forest bird species in the six age classes were recorded within 30m on both sides of the transects. For use in my study, I omitted species that were encountered only one time during the survey to reduce the number of vagrant species. I also omitted nonforest species (sometimes these were detected in the youngest age classes; Raman et al. 1998). I then divided the remaining species into two categories: (1) forest specialist species and (2) forest generalist species and modeled the recovery of each category separately.

I modeled the colonization and extinction processes of a species as a binomial process. A nonlinear regression equation was built with the number of forest specialist species as the dependent variable and forest age as the independent variable using Proc NONLINEAR in SAS (SAS v.9.00, 2002):

$$y_i = \frac{44.8187i}{6.1084 + i} \tag{1}$$

where y<sub>i</sub> is number of forest species at age i of succession.

Based on the above equation, I calculated the yearly turnover rate  $(p_i)$  defined as the probability that a species colonizes a forest stand minus the probability that a species goes extinct from the stand:

$$y_{i+1} - y_i = \sum_{j=0}^{Y-round(y_i)} {\binom{Y-round(y_i)}{j}} * p_i^{j} * (1 - p_i)^{Y-round(y_i)-j} * j$$
(2)

where  $y_i$  is the number of forest specialist species in a forest of age i obtained using equation 1. Y is the total forest specialist species pool, thus Y-round( $y_i$ ) is the number of species in the pool that have not yet recovered in a forest stand of age i  $p_i$  is the probability that a species colonizes a forest stand minus the probability that a species is extinct from the stand of age i.

The right hand side of the equation is the expected increase in number of species in a forest stand of age i. The left hand side of the equation is the increase in the number of species in the stand in age i, obtained using equation (1).

Similarly, a nonlinear regression equation was built with the number of forest generalist species given in the study by Raman et al. (1998) as the dependent variable and forest age as the independent variable using Proc NONLINEAR in SAS (SAS v.9.00, SAS 2002):

$$z_i = \frac{35.5715i}{1.3601+i} \qquad (3)$$

where  $z_i$  is number of forest species at age i of succession.

Based on the above equation, I calculated the yearly turnover rate  $(g_i)$  defined as the probability that a species colonizes a forest stand minus the probability that a species is extinct from the stand:

$$z_{i+1} - z_i = \sum_{j=0}^{Z-round(z_i)} {\binom{Z-round(z_i)}{j}} * g_i^{j} * (1 - g_i)^{Z-round(z_i)-j} * j$$
(4)

where  $z_i$  is the number of forest generalist species in a forest of age i obtained using equation 3. Z is the total forest generalist species pool, thus Z-round( $z_i$ ) is the number of

species in the pool that have not yet recovered in a forest stand of age i.  $g_i$  is the probability that a species colonizes a forest stand minus the probability that a species is extinct from the stand of age i.

The right hand side of the equation is the expected increase in number of species in a forest stand of age i. The left hand side of the equation is the increase in the number of species in the stand in age i, obtained using equation (3).

Equations (2) and (4) were solved over a time horizon of 300 years for p<sub>i</sub> and g<sub>i</sub>. I then generated a random number (from 0 to 1) for each species and individually compared the number with p<sub>i</sub> or g<sub>i</sub> to determine whether a forest specialist species or generalist species, respectively, was added to the stand of age i in a particular year. After each logging event, the age of the stand was adjusted using the forest growth model, and the number of bird species in each category was adjusted accordingly using equations (1) and (3). A total of 1000 simulations were run for each logging scheme. The average number of species supported just before the last logging event of simulation was calculated and compared among logging schemes. All calculations were done using MatLab R2006a (The MathWorks, Inc. 2006).

Several additional assumptions were needed. These were:

- The forest growth model is valid.
- Detection probabilities among different habitat types in the study by Raman (1998) were equal to one.
- Individual bird species within the same category (forest specialist or forest generalist) have the same turnover rate for a given forest age.
- The recovery of a species is independent of other species.

- The source for avian community recovery is sufficient.

# RESULTS

In the simulation of forest growth clear cut (WF = 0) and logging cycles of 50 or 100 years, the rate of recovery of forest species is very rapid during early stages of forest succession (Fig. 3.1a, b). The recovery rate of forest generalists is very high during the first 15 years of succession and then starts to become asymptotic. The recovery rate of forest specialists remains high until about 50 year of succession (Fig. 3.1a, b). After 50 years, the rate slows, and only a few more bird species are added to the forest stand in future years.

The forest generalists are not affected much by forest logging even at short logging cycles and with small amounts of wood volume left after cutting (Fig. 3.1c). Roughly, logging schemes with either LC > 10 years or WL > 25% will result in 70% of the forest generalist species pool being conserved. Logging schemes with either LC > 70years or WL > 60% will result in 80% of the forest generalist species pool being conserved (Fig. 3.2, Table 3.1). This is the maximum number of species that can be conserved within a forest stand at a particular age. Logging schemes with longer logging cycles and more wood left after harvesting do not increase the recovery of forest generalists because the colonization and extinction rates tend to be equal at later succession stages (Fig. 3.2).

Logging with short logging cycles and small amounts of wood left after harvesting seriously affect forest specialist species (Fig. 3.1c). Logging schemes with either LC > 20 years or WL > 35% will result in 70% of the regional forest specialist

species pool being conserved (Fig. 3.3, Table 3.2). To conserve 80% of the regional forest specialist species, logging schemes with either LC > 35 years or WL > 50% should be implemented. For overall species richness, logging schemes with large amounts of wood left after harvesting do not greatly affect the total species richness (Fig. 3.1e, f). In logging schemes with small amounts of wood left after harvesting, bird communities can recover if cutting rotation intervals are long enough (Fig. 3.1a, b, d). The most severe effect on the bird communities occurs if short logging schemes with either LC > 15 years or WF > 30% will result in 70% of the regional forest bird species pool being conserved (Fig. 3.4, Table 3.3). To conserve 80% of forest bird species pool in the region, logging schemes with either cycle lengths > 40 years or WF > 55% should be implemented. Additional logging schemes and how they affect bird communities are shown in Tables 3.1, 3.2, and 3.3.

## DISCUSSION

Several assumptions were needed for my modeling efforts. The first assumption is that the forest growth model is valid. MYRLIN (Alder et al. 2002) was developed to specifically model the growth of evergreen forest in the tropics. The results from MYRLIN are used as guidelines for harvest regulation and forest management (Alder et al. 2002), and are probably reliable. There is a strict relationship between forest biomass and forest age, therefore, adjusting the age of the forest based on its stand wood volume is also reasonable. The second assumption is that bird detection probabilities among different habitat types in the study by Raman (1998) were equal to one. Bird surveys were conducted ten times on each transect, therefore, all species were likely detected with these numerous surveys. In similar survey work, I found that species detection probabilities were 0.25 per survey (Vu, chapter 1). Extrapolating these results to 10 visits results in a detection probability of  $0.95 \approx 1$ , supporting this assumption. The third assumption is that bird species in the same category have the same turnover rate at a given forest age. I modeled some heterogeneity by considering forest generalists and specialists separately, however some additional individual heterogeneity could still be present. The fourth assumption is that recovery of a species is independent of other species. The recovery of a species is most likely to be dependent on another species if a strong ecological relationship between the species exists. However, many avian species occupy the same trophic levels suggesting that there are few cases in which the recovery of two species is dependent on each other. For example, if the first species is the prey of the second species, then the recovery of the second species will be dependent on that of the first one. Secondary cavity nesters depend on the nest hole made by other species; therefore, the recovery of these species depends on the recovery of primary cavity nesters. However, these secondary cavity nesters are not common. The fifth assumption is that the source of species for community recovery is sufficient. Birds are generally more mobile than other taxa so that they can colonize very distant sites, so this assumption might be met. However, in logging layout design, I recommend that the logged stands should be designed to be close to other stands at later succession stages to assure that the source of species for community recovery will be sufficient.

The recovery rate of forest generalists is very high during the first 15 years of succession and then starts to become asymptotic (Fig. 3.1a, b). This is due to the broad

habitat requirements of forest generalists. Therefore, the forest generalists are not affected much by forest logging even at short logging cycles and small amounts of wood volume left after cutting (Fig. 3.1c, Fig. 3.2). The maximum number of forest generalist species can be conserved if logging schemes with LC > 70 years or WL > 60% are implemented (Fig. 3.2, Table 3.1). Further increases in logging cycle lengths and increases in wood volume left after cutting do not increase the recovery of forest generalists because the colonization rate and extinction rate tend to be equal at later succession stages (Fig. 3.1e, f and Fig. 3.2). Therefore, increases in logging cycles and increases in wood volume left after cutting beyond these thresholds may not be necessary to conserve forest generalist bird species.

Logging affects total bird species richness mostly though influencing the number of forest specialists (Fig. 3.1a, b, c, d). Forest bird species, especially specialist species, decreases sharply right after forest logging with high intensity and this is supported by other findings (Mason 1996, Holbech 2005). Intense logging most likely reduces the complexity of the vegetation structure and other resources. However, bird communities then recover strongly over the next 40-50 years. Dunn (2004b), in a review paper, found that generally the avian species richness will completely recover 20 years after clear cutting in tropical evergreen forest and this finding is also supported by my simulation results. Several other studies have also found high recovery rates in avian communities in forests that were cleared and then abandoned for 10-20 years (Andrade and Rubiotorgler 1994, Duengkae and Chimchome 2007). The slowing rate of recovery in the late succession stages can be attributed to several factors: (1) few bird species are not represented in the forest stand; and (2) the lower rate of change in forest structure at late succession stages. The lower rate of change in forest structure inhibits new species from colonizing the forest stand because of the limited niche space available. This general trend of increasing bird species richness with the maturity of vegetation has been supported by many other studies (Lack 1933, Urban and Smith 1989, Blake and Loiselle 1991).

I found that logging schemes with low intensities do not greatly affect bird communities because only a small number of the largest trees are cut; my findings are similar to those of others (Aleixo 1999, Dunn 2004a). Forests that have undergone a low-intensity logging event still have a good canopy formed by middle-size trees, and the understory is still dense. Therefore, birds depending on the understory and middle canopy may not be much affected (Dale and Slembe 2005).

Although tropical forests are very rich in biodiversity, these forests are still used for economic gain. To balance economic gain with conservation, forests outside protected areas (e.g., national parks where no logging is allowed) can be harvested but under careful considerations. To minimize the effect of forest cutting on bird communities while still accruing the economic gains of logging, logging schemes should be adroitly selected. Roughly, logging schemes with either LC > 40 years or WL > 55% will result in 80% of overall forest bird species pool in the region will be conserved (Fig. 3.4, Table 3.3). These logging scheme thresholds can be met if sustainable forest production methods are followed. Sustainable forest harvesting is obtained if the logging cycle is longer than 60 years and wood volume left is more than 20% (Kammesheidt et al. 2001). By harvesting forests in this way, the associated bird communities in the forest will also likely be conserved at a maximum level.

Finally, my modeling efforts have been at the community level and have not focused on any specific species; therefore, if there are specific species of important conservation concern, the conservation action plan for that species should be based on more specific study of those species. Further field validation of the results of my modeling efforts will strengthen the application of my results.

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WL	LC (year)														
(%)	1	5	10	15	20	25	30	35	40	45	50	55	60	65	70
0	34.1	63.8	70.7	74.0	75.5	76.7	77.4	77.5	78.1	78.7	78.7	78.8	79.1	79.0	79.0
5	54.5	67.1	71.8	74.2	75.5	76.3	76.9	77.5	77.7	77.9	78.2	78.3	78.6	78.9	79.0
10	61.4	69.9	74.0	75.9	76.8	77.8	78.5	78.6	78.9	79.2	79.4	79.6	79.4	80.1	80.4
15	63.6	70.4	73.9	75.4	76.6	77.4	77.6	78.2	78.6	78.6	78.9	79.2	79.2	79.2	79.3
20	65.9	71.2	74.3	75.7	76.5	77.4	78.0	78.2	78.3	78.9	78.8	79.0	79.3	79.5	79.4
25	70.5	73.4	75.2	76.5	77.2	77.9	78.2	78.7	78.9	79.1	79.3	79.2	79.4	79.3	79.6
30	72.7	74.3	75.5	76.2	77.0	77.2	77.6	78.0	78.0	78.2	78.3	78.5	78.7	78.6	78.5
35	75.0	75.8	76.8	77.3	77.6	78.0	78.3	78.4	78.5	78.8	78.8	79.1	79.2	79.0	79.3
40	77.3	77.9	78.4	78.8	79.0	79.3	79.5	79.8	79.9	80.0	80.1	80.1	80.0	80.2	80.4
45	77.3	77.7	78.1	78.4	78.6	78.8	79.0	79.2	79.3	79.4	79.5	79.5	79.8	79.8	79.7
50	77.3	77.5	77.9	78.1	78.4	78.5	78.7	78.8	79.0	79.0	79.0	79.1	79.2	79.2	79.2
55	77.3	77.5	77.7	77.9	78.1	78.3	78.5	78.6	78.7	78.7	78.8	78.8	78.9	78.9	79.0
60	79.5	79.7	79.9	80.0	80.2	80.2	80.4	80.5	80.5	80.6	80.6	80.6	80.7	80.9	80.8

Table 3.1. Percentage of the forest generalist bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).

WF	LC (year)														
(%)	1	5	10	15	20	25	30	35	40	45	50	55	60	65	70
0	12.8	42.5	59.1	67.3	72.9	75.8	79.1	80.6	82.3	83.9	84.8	85.4	86.3	87.2	87.4
5	31.9	51.2	63.5	70.4	74.6	77.7	80.2	81.8	83.4	84.5	85.5	86.0	86.9	87.5	88.0
10	38.3	54.5	65.4	71.6	75.5	78.5	80.7	82.1	83.6	84.4	85.4	86.1	87.0	87.8	88.0
15	42.6	56.3	65.9	71.9	76.0	78.4	80.8	82.2	83.7	85.0	85.5	86.2	86.8	87.3	88.1
20	46.8	58.7	67.7	73.0	76.5	79.1	80.8	82.3	83.8	84.7	85.7	86.5	87.0	87.4	88.0
25	57.4	65.4	71.7	75.7	78.7	80.7	82.1	83.8	84.8	85.6	86.4	87.0	87.7	88.1	88.5
30	66.0	70.8	74.8	77.8	80.3	82.0	83.4	84.2	85.4	86.1	86.7	87.2	87.8	88.3	88.6
35	72.3	75.4	78.6	80.4	82.0	83.6	84.7	85.6	86.4	86.9	87.7	88.0	88.4	88.9	89.3
40	76.6	78.9	80.9	82.6	83.8	85.1	86.2	86.6	87.3	87.9	88.3	88.6	89.2	89.5	89.6
45	78.7	80.3	82.0	83.4	84.5	85.6	86.2	86.9	87.5	88.0	88.6	88.8	89.6	89.5	89.7
50	80.9	82.1	83.4	84.6	85.3	86.2	86.9	87.6	88.0	88.3	88.9	89.0	89.5	89.7	90.0
55	83.0	84.0	85.0	85.7	86.5	87.1	87.7	88.2	88.6	88.8	89.2	89.6	89.9	90.0	90.4
60	85.1	85.8	86.6	87.4	87.7	88.3	88.7	89.2	89.5	89.8	90.0	90.2	90.5	90.8	91.0

Table 3.2. Percentage of the forest specialist bird species pool recovered species as a function of logging cycle length (LC) and wood volume left after harvesting (WL).
WF (%)	LC (year)														
	1	5	10	15	20	25	30	35	40	45	50	55	60	65	70
0	23.1	52.8	64.7	70.5	74.2	76.2	78.3	79.1	80.3	81.4	81.9	82.2	82.8	83.2	83.4
5	42.9	58.9	67.5	72.2	75.1	77.0	78.6	79.8	80.6	81.3	82.0	82.3	82.9	83.3	83.6
10	49.5	61.9	69.6	73.7	76.2	78.2	79.6	80.4	81.4	81.9	82.5	83.0	83.3	84.0	84.3
15	52.7	63.1	69.8	73.6	76.3	77.9	79.2	80.3	81.2	81.9	82.3	82.8	83.1	83.4	83.8
20	56.0	64.7	70.9	74.3	76.5	78.3	79.4	80.3	81.2	81.9	82.4	82.9	83.3	83.6	83.8
25	63.7	69.3	73.4	76.1	78.0	79.3	80.2	81.3	81.9	82.5	83.0	83.3	83.7	83.9	84.2
30	69.2	72.5	75.1	77.0	78.7	79.7	80.6	81.2	81.8	82.3	82.6	83.0	83.4	83.6	83.7
35	73.6	75.6	77.7	78.9	79.9	80.9	81.6	82.1	82.6	83.0	83.4	83.7	84.0	84.1	84.5
40	76.9	78.4	79.7	80.8	81.5	82.3	82.9	83.3	83.7	84.0	84.3	84.5	84.8	85.0	85.2
45	78.0	79.0	80.1	81.0	81.7	82.3	82.7	83.2	83.5	83.8	84.2	84.3	84.9	84.8	84.9
50	79.1	79.9	80.7	81.4	81.9	82.5	83.0	83.3	83.6	83.8	84.1	84.2	84.5	84.6	84.8
55	80.2	80.8	81.5	81.9	82.4	82.9	83.3	83.5	83.8	83.9	84.2	84.4	84.6	84.6	84.8
60	82.4	82.9	83.4	83.8	84.1	84.4	84.7	85.0	85.1	85.4	85.5	85.6	85.8	86.0	86.1

Table 3.3. Percentage of the total forest bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).



Figure 3.1a-f. Simulations of bird community dynamics along a succession gradient of a tropical evergreen forest under different logging schemes. LC = logging cycle, WL = wood volume left after harvesting.



Figure 3.2. Percentage of the forest generalist bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).



Figure 3.3. Percentage of the forest specialist bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).



Figure 3.4. Mean percentage of the total forest bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).

# **CHAPTER 4**

#### AVIAN MALARIA IN WILD BIRDS IN NORTHERN VIETNAM

Abstract: Wildlife diseases are gaining increasing attention given concerns over the role humans may play in emerging wildlife diseases and the impacts pathogens may have on vulnerable wildlife populations (Daszak et al. 2004). The avian blood parasites, or haemosporidia, make up one such group of parasites linked to critical conservation concerns. Given these conservation concerns and a paucity of information on avian blood parasites in birds in Vietnam, my study was aimed at characterizing the sample prevalence of avian blood parasites that cause avian malaria and investigating the ecological factors affecting prevalence in free-ranging wild land birds. I focused on two genera of blood parasites including *Plasmodium spp.* and *Haemoproteus spp.* that cause malaria in birds. The samples were collected in Cuc Phuong and Tam Dao National Parks, northern Vietnam in summer 2007 and 2008. The overall prevalence of avian malaria (AM) in sample birds was 45.85%. Infections were detected in the majority of bird species sampled. The sample prevalence did not differ by sampling regions and habitats. However, higher parasite prevalence was observed in flocking species compared to solitary species and higher parasite prevalence was observed in adult birds compared to juvenile birds. This is the first documented occurrence of AM in Vietnam. Given the high prevalence and the broad host distribution of AM, I would recommend additional studies to strengthen the data set for inferences about sociality and to

investigate the effects of other untested covariates on AM prevalence. Additionally, studies of the physiological, behavioral, and ecological costs of parasitism by AM parasites on birds in natural environments should be conducted. A further phylogenetic analysis of AM parasites detected during my study may reveal new species or lineages of avian malarial blood parasites.

# **INTRODUCTION**

Wildlife diseases are gaining increasing attention given concerns over the role humans may play in emerging wildlife diseases and the impacts pathogens may have on vulnerable wildlife populations (Daszak et al. 2004). To date, disease has led to the extinction of at least 31 animal species, of which 18 are avian species (Smith et al. 2006). In addition, the IUCN Red List includes 223 critically endangered animal species with disease as a 'contributing factor' (Smith et al. 2006). The avian blood parasites, or haemosporidia, make up one such group of parasites linked to critical conservation concerns. Avian blood parasites, including those that cause avian malaria, have been implicated in the decline or loss of many bird populations including extinctions of 13 Hawaiian endemic forest bird species (Atkinson et al. 2000, Smith et al. 2006, Van Riper et al. 1986).

Blood parasite species in the phylum Apicomplexa, including the genera *Haemoproteus, Plasmodium*, and *Leucocytozoon*, are known to infect at least 282 species from 23 orders of birds (Valkiunas 2004). Of these three genera, *Haemoproteus* and *Plasmodium* cause malaria in birds. These parasites are transmitted among birds by blood-sucking dipterans. The effects of avian malarial parasites on hosts are very diverse. Disease symptoms of avian malaria can be unapparent, mild, or severe. In severe cases, anemia, reduced food consumption, and weight loss can result in high mortality (Atkinson et al. 2000, Tompkins and Gleeson 2006). Translocated animals are among the most seriously affected (Valkiunas 2004). In natural environments, the effects of blood parasite infections on birds are usually underestimated because ill and dead birds are difficult to detect (Valkiunas 2005).

The presence of avian blood parasites has been recorded in all parts of the world (Valkiunas 2005). Laird (1998) documented the presence of *Plasmodium spp*. in birds in tropical Asia; however, other genera of avian blood parasites have not been studied there. Additionally, no studies have characterized avian malarial parasites in Indochina, including Vietnam, an area very rich in biodiversity and endemism (Nhat 2001).

Human encroachment and land use changes have been thought to be attributed to many emerging diseases that contribute to the declines of wildlife species (Daszak et al. 2001). Human encroachment and land use changes have contributed to the emergence of diseases in wildlife by bringing pathogens and their vectors to new areas, by bringing human and domestic animals closer to wildlife, and by changing the ecology of wildlife species (Daszak et al. 2001). For example, agricultural operations and deforestation have increased the prevalence of some wildlife diseases by increasing the occurrence of vectors, specifically mosquitoes (Leisnham et al. 2004, Reiter and Lapointe 2007). In particular, agricultural development and deforestation can alter vector populations by creating more favorable environmental conditions for breeding (Leisnham et al. 2004, Reiter and Lapointe 2007). In Vietnam, land use has recently changed considerably with the replacement of natural forests by agricultural and urban land use types (Nhat 2001). This leads to the dual concerns of habitat loss as well as emerging diseases affecting the avifauna of Vietnam.

Given these conservation concerns and a paucity of information on avian malarial parasites in birds in Vietnam, my study focused on the following objectives: (1) characterizing the sample prevalence of avian malaria (*Plasmodium spp.* or *Haemoproteus spp.*) in free-ranging wild land birds in northern Vietnam, and (2)

examining factors affecting the sample prevalence of blood parasites in free-ranging wild land birds among three habitat types including forest interior, forest edge, and human dominated landscape. Birds living in forest interiors are likely to have reduced exposure to vectors (Leisnham et al. 2004, Reiter and Lapointe 2007); given this, I predict that the prevalence of blood parasites in birds in forest interiors will be lower than for birds in forest edges and prevalence will be highest for birds in human-dominated landscapes. The effects of other covariates including flocking behavior (a measure of sociality) and age will also be examined. I predict that flocking birds will have higher parasite prevalence than solitary birds because sociality is believed to enhance the transmission of disease pathogens among animals (Cote and Poulin 1995, Dobson 1988, Freeland 1976). Adult birds have a longer time of exposure to the parasites (Ricklefs et al. 2005) relative to juveniles so I predict that the prevalence will be higher in adult birds. Lastly, potential differences in prevalence in the two sampling region will be investigated.

#### **METHODS**

#### **Study sites**

The research was conducted in Cuc Phuong National Park (CPNP;  $20^{\circ} 14' - 20^{\circ}$ 24' N;  $105^{\circ} 29' - 105^{\circ} 44'$  E; Appendix I) and Tam Dao National Park (TDNP;  $21^{\circ} 21' - 21^{\circ} 42'$  N;  $105^{\circ} 23' - 105^{\circ} 44'$  E; Appendix I) in northern Vietnam. The study area within TDNP is comprised of regrown forests that had been clearcut for cultivation in the past while CPNP has not experienced similar cultivation practices. Study areas within the two parks were located at or below 300m in elevation. The two parks have a tropical climate with two distinctive seasons driven by monsoon winds. The hot and rainy season extends from April to November while the cool and dry season is from December through March. The two parks are surrounded by rural areas. Many people living near the parks rely on subsistence farming. Each family rears fowl (i.e., chickens and ducks) for their own consumption or for trade. Rice fields and ponds have also been created in and around human-dominated landscapes. Chemical pesticides are widely used in agricultural cultivation, including subsistence operations, and can possibly affect the reproduction of potential vectors.

# Sample collection

Blood samples were collected at Cuc Phuong National Park from June to July 2007 and at Tam Dao National Park in July 2008. Free-ranging birds from various families were captured by mist nets for each habitat type including forest interior, forest edge, and human-dominated landscapes. Sampling efforts were based on time available in the field and permission to access lands. Birds were aged (juvenile or adult) based on feather characteristics and classified to species following Robson (2005). I collected small blood samples via jugular venipuncture. Blood smears were made, fixed with methanol, and stained later with a modified Giemsa kit (Jorgensen Laboratories Inc., Loveland, CO). Blood samples were also stored on lysis buffer (1M Tris, pH 8.0, 0.5M EDTA pH 8.0, 5M NaCl, and 10%SDS) for transportation to the laboratory for subsequent analysis.

#### **Molecular Analysis**

Genomic DNA was extracted from the blood samples using DNeasy extraction kits (Qiagen, Valencia, California) following manufacturer's instructions. I electrophoresed 5-7µL of the extract on a 1.5% agarose gel followed by ethidium bromide staining and UV visualization to assess the presence of DNA in the extracts. DNA was extracted from a second aliquot for samples with no or very low quality DNA.

Samples were screened for infection based on the presence or absence of avian malarial DNA using the primer set, F2/R2, designed to detect DNA of *Plasmodium spp*. or *Haemoproteus spp*. (Beadell et al. 2004). This primer set has been used on a wide range of avian hosts (e.g.,Beadell et al. 2004, Ishtiaq et al. 2007) and is thought to be specific to these two avian malarial parasite genera and not to other blood parasite genera such as *Leucocytozoon, Trypanosoma*, and *Hepatozoon* parasites. F2/R2 amplifies a 132bp region of the parasite cytochrome b region of the mitochondrial genome.

PCR amplifications for a portion (n = 45) of the samples were carried out on 1.8  $\mu$ L of extracted DNA in 25 $\mu$ L volumes following conditions outlined in Beadell and Fleischer (2005). The final concentrations of components for these reactions were as follows: 0.6 $\mu$ M each primer, 1X PCR Gold buffer (Applied Biosystems), 2.0mM MgCl<sub>2</sub>, 0.8 mM dNTPs, 0.8 mg/mL BSA, and 0.5 units of AmpliTaq Gold DNA polymerase (Applied Biosystems). The remainder of the reactions (n = 385) were on 1.5 $\mu$ L of extracted DNA using illustra<sup>TM</sup> puReTaq Ready-To-Go beads (GE Healthcare, Piscataway, NJ) with final primer concentrations of 0.5  $\mu$ M of each primer. Several negative controls (i.e., water instead of sample) were included in each PCR bout to check for contamination and at least one positive control (aliquots from blood samples known to have *Plasmodium spp.* or *Haemoproteus spp.*) was also included.

All amplifications were conducted with an initial denaturing step for 8 min at 94°C followed by 35 cycles under the following conditions, denaturation for 30 s at 92°C, annealing for 30 s at 52°C, and extension for 30 s at 72°C, followed by a final extension for 7 min at 72°C.

To identify samples that were positive for avian malarial DNA, 15 µL of the amplicon were electrophoresed on a 2% agarose gel followed by ethidium bromide staining and UV visualization. A 100bp size marker ('ladder'; New England Biolabs, Pswich, MA) was included in at least one lane on each gel for size comparison. A positive sample was identified by the presence of a band of the appropriate size (i.e., 132bp) on gels. PCR reactions and electrophoresis were repeated 2 to 4 times on samples with equivocal results (i.e., very faint bands or smeared bands) and the consensus result was used for analysis. Samples that failed to extract or amplify were omitted from the analyses.

#### Data analysis

Data on the percentage of positive samples out of total samples were analyzed using Proc LOGISTIC (SAS v.9.00, SAS 2002). I constructed 32 models including four main effect models including: (1) prevalence (Prev) is equal among the three habitat types Ha<sub>(FI=FE=HL)</sub>, (FI = forest interior, FE = forest edge, and HL = human dominated landscape); (2) equal prevalence in forest interior and forest edge, with human-dominated landscape being different Ha<sub>(FI=FE#HL)</sub>; (3) equal prevalence in forest edge and humandominated landscape, with forest interior being different Ha<sub>(FI#FE=HL)</sub>; and (4) different prevalence for each of the three habitat types Ha<sub>(FI#FE#HL)</sub>. Additionally, covariate effects of flocking behavior (Fb) and age (Ag) were also included in the models. A species that forages predominately in a flock was given a value Fb=1, and solitary species or species living in pairs during the breeding season were assigned a value Fb=0. Species were designated as flocking or solitary using Rasmussen and Anderton (2005) and personal experience. Prevalence was also modeled as constant over sampling region (Sr) (CPNP vs TDNP) and varying by sampling region. Akaike's Information Criteria (AICc) was used for model selection in investigating the factors that influence avian malarial parasite prevalence. Additionally, AICc weights (w), cumulative AICc weights ( $w_i$ ) and parameter estimates were used to assess the models (Burnham and Anderson 2002). Estimates of prevalence were model-averaged across the entire model set if multiple models had non-trivial AICc weights (Burnham and Anderson 2002).

### RESULTS

Samples were collected from 266 birds in CPNP in summer 2007 and 158 birds were sampled in TDNP in summer 2008. Of the total samples, screening results were produced for 256 birds from CPNP and 154 birds from TDNP (Appendix III). These birds represented 61 species and 15 families. One hundred and sixteen birds caught in CPNP tested positive for avian malarial parasites, producing a sample prevalence of 45.31%. Seventy two birds caught in TDNP tested positive, producing a sample prevalence of 46.75%. The overall sample prevalence of the combined dataset was 45.85%. Of 22 species with at least five sampled individuals, avian malarial infections were detected in 21 species. No single model explained the sample blood parasite prevalence adequately (Table 4.1). A model in which sample prevalence was influenced by an additive combination between flocking behavior and age had the strongest support, with w = 0.27. All other models had much lower support. Flocking behavior and age also consistently appeared in the top models. Additionally, by examining the cumulative AICc weights  $(w_i)$ , there was strong evidence that variation in prevalence was influenced by flocking behavior  $(w_i = 0.79)$  and age  $(w_i = 0.94)$ . Flocking birds had higher sample prevalences than solitary bird species (Fig. 4.1). Adult birds also had a higher prevalence than did juvenile birds (Fig. 4.1).

Habitat had a much smaller effect on avian malarial blood parasite prevalence; habitat did not appear in the top models as frequently as flocking behavior and age (Table 4.1 and Fig. 4.1). Sampling region had the least effect on prevalence as this covariate did not appear in the top three models and had a small cumulative AICc weight ( $w_i = 0.27$ ). Accordingly, the overall estimate of sample prevalence for birds captured at Cuc Phuong National Park (45.31%) is similar to that of Tam Dao National Park (46.75%).

#### DISCUSSION

The overall avian blood parasite prevalence of 45.85% is similar to several other findings using the same and additional PCR primers for screening (Ishtiaq et al. 2007, Murata et al. 2008). The high percentage of species that were positive for avian malarial parasites in this study further supports the idea of a cosmopolitan host distribution for these parasites (Beadell et al. 2004). Sample prevalence did not differ between the two sampling regions (CPNP and TDNP) which can be explained by the similarity of climatic conditions of the two study areas. CPNP and TDNP are both located in northern Vietnam at similar latitude and experience a similar wet tropical climatic regime. Sampling sites within the two regions were both lower than 300m in elevation and sampling was balanced among habitat types at both Parks. Additionally, birds were captured at the two sites during the same season, just in different years.

Similarly, avian blood parasite prevalence did not differ by habitat type. My results did not support the hypothesis that blood parasite infection in birds inhabiting the human dominated landscapes might be higher than in birds inhabiting forests as several studies in New Zealand suggest (Leisnham et al. 2004, Reiter and Lapointe 2007). In contrast to temperate New Zealand, the microclimate of the dense tropical forests in northern Vietnam is characterized by high relative humidity and abundant standing water, both factors that would support the rapid reproduction and development of dipteran vectors (Aruch et al. 2007). Additionally, chemical pesticides are widely used in agricultural practices near the study sites which might account for lower-than-expected prevalences in human-dominated landscapes due to potentially reduced reproduction of mosquitoes. Parasite prevalence varied by host species, thus an improvement to better reveal the effects of habitat on prevalence would be to focus on host species that are common to all three habitats, or, a group of host species that has similar ecological and behavioral traits.

Sociality is believed to enhance the transmission of disease pathogens among animals (Cote and Poulin 1995, Dobson 1988, Freeland 1976). The higher prevalence

among flocking birds in my study supports this hypothesis (Fig. 4.1). Flocks of Redwhiskered Bulbul, Black-crested Bulbul, Light-vented Bulbul, Striped Tit Babbler, Scalybreasted Munia or Japanese White-eye can have dozens of individuals. In the tropics during the non-breeding season when birds are likely to be roosting or moving locally together, these species can also join mixed-species flocks that can contain many individuals of several species (Lee et al. 2005). Although, according to the encounterdilution effect idea, birds living in flocks might have fewer bites per capita by vectors than solitary birds (Hart 1997). However, that idea has limited empirical support in birds. Additionally, the encounter-dilution effect might work for such cases in which the density of vectors is low. Vectors are very abundant in the tropics, per capita number of bites per bird might not be reduced by increasing the number of birds within a flock. Large flocks of birds might also be more attractive to and easier to be detected by vectors than solitary birds. The higher local density of birds in the flock may also enhance the transmission of the pathogen if transmission in this system is density-dependent (Anderson and May 1979).

Avian malaria prevalence in adult birds was estimated to be higher than in juvenile birds (Fig. 4.1). Other studies report conflicting findings about blood parasite prevalence in adults and juvenile birds. Durrant et al. (2008) and Ribeiro et al. (2005) found similar overall prevalence between adult birds and juvenile birds while Ricklefs et al. (2005) found overall prevalence to be higher in adult birds compared to juvenile birds. Similarly, the sample prevalence of blood parasites in adults in my study is much higher than in juveniles. Hypotheses that support higher prevalence in juvenile birds are that juvenile birds might have undeveloped protection mechanism to biting vectors such as

behavioral response, immobile locomotion (Valkiunas 2005), undeveloped plumage, and reduced ability to inhibit the development of blood parasites once infected (Ricklefs et al. 2005). However, another hypothesis that supports the idea of higher prevalence in adult birds is that adult birds are more likely to be infected because they have had a longer time during which they can get bitten by vectors, become infected, and accumulate parasites. Once infected, the infection can persist in birds for years or even the lifetime of the bird (Atkinson and Van Riper III 1991). Additionally, it usually takes several weeks after infection for the parasite to appear in the peripheral blood. Juvenile birds up to a few weeks old can be infected with the parasites but do not express them in peripheral blood for detection (Atkinson and Van Riper III 1991, Ricklefs et al. 2005), particularly *Haemoproteus spp.* that require asexual schizogony in non-circulating blood cells before being expressed as gametocytes in peripheral blood.

In conclusion, the blood parasite prevalence in the birds I sampled is relatively high. Infections were detected in the majority of species sampled. The sample prevalence did not differ by sampling regions and habitats. However, higher parasite prevalence was observed in flocking species compared to solitary species. Higher parasite prevalence was also observed in adult birds compared to juvenile birds. Given the high prevalence, the broad host distribution of AM, and the paucity of information on the ecology of AM, I would recommend additional studies to look at how parasite prevalence varies across seasons and to strengthen the data set for inferences about sociality. Further, I suggest investigating the effects of other untested covariates such as foraging height, nesting height, and nest structure. Additionally, studies of the cost of parasitism on birds in natural environments should be conducted. The cost of parasitism

can be expressed through physiological, behavioral, and ecological traits (Atkinson and Van Riper III 1991) such as survival, fecundity, and foraging performance. In those studies, Japanese White-eyes could be a useful target species because this species is abundant, easy to catch, and has high parasite prevalence.

Until recently, microscopy was used to identify infections in birds. This technique underestimated true prevalence because infections from birds with low parasitemias were very difficult to detect (Ribeiro et al. 2005); parasite infection can thus be missed by chance alone due to the fact that parasitemias can vary within a blood smear or among blood smears. The underestimation of prevalence is more important when smears are not in good condition due to harsh field conditions (Valkiunas et al. 2008). Molecular techniques improve estimates of prevalence because they rely on PCR which amplifies DNA, even from very low starting concentrations. Nevertheless, infections can be missed because some primer pairs do not detect some lineages of AM parasites (J.S. Beadell, pers. comm.). The problem with underestimation of prevalence due detection failures might be solved using parameter estimation techniques that take into account the probability of detection probability such as capture-recapture.

As a final direction for future work, phylogenetic analysis of the parasites I detected should be conducted. My study focused on detecting the presence of blood parasites in two genera: *Haemoproteus* and *Plasmodium* but I did not classify the parasite to species. This is the first study of AM parasites in birds inVietnam and my results suggest that an extraordinary high number of bird species harbor blood parasites. It is likely that additional analysis of AM parasites detected during my study will reveal new species or lineages of blood parasites. Because only 61 avian species (equivalent to 7.2%)

number of bird species in Vietnam) were studied, and several species had only one or a few individuals sampled, studies directed to species that have not been sampled in this study will reveal a broader picture of AM in avifauna in Vietnam.

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Table 4.1. Model selection results for 32 models describing the sample prevalence of avian malaria (Prev = Prevalence, FI = forest interior, FE = forest edge, and HL = human dominated landscape). The model set includes four main effect models (1) prevalence is equal among the three habitat types Ha<sub>(FI=FE=HL)</sub>; (2) equal prevalence in forest interior and forest edge, with human-dominated landscape being different Ha<sub>(FI=FE#HL)</sub>; (3) equal prevalence in forest edge and human-dominated landscape, with forest interior being different Ha<sub>(FI#FE=HL)</sub>; and (4) different prevalence for each of the three habitat types Ha<sub>(FI#FE#HL)</sub>. Covariate effects of flocking behavior (Fb), age (Ag) and sampling region (Sr) were also used to model the sample prevalence separately or in combination. Models are ranked by AICc.  $\Delta$ AICc is the difference in AICc units from the highest ranking model. AICc weights (*w<sub>i</sub>*), model likelihood (L), -2Loglikehood (-2LogL), number of parameters (K), and deviance (D) are also shown. Model likelihood is the likelihood of a model relative to the other models. AICc weights sum to one and models with higher likelihood have more weight. Deviance is the difference in (-2log × likelihood) of the current model and (-2log × likelihood) of the saturated model.

Model	AICe	<b>AAICc</b>	W <sub>i</sub>	L	-2LogL	K	D
Prev = Fb + Ag	557.72	0.00	0.27	1.00	551.66	3	0.60
$Prev = Ha_{(FI \# FE = HL)} + Fb + Ag$	559.21	1.49	0.13	0.47	551.11	4	0.05
$Prev = Ha_{(FI = FE \# HL)} + Fb + Ag$	559.70	1.99	0.10	0.37	551.61	4	0.55
Prev = Sr + Fb + Ag	559.74	2.02	0.10	0.36	551.64	4	0.59
Prev = Ag	560.71	2.99	0.06	0.22	556.68	2	5.62
$Prev = Ha_{(FI \# FE \# HL)} + Fb + Ag$	561.21	3.50	0.05	0.17	551.07	5	0.01
$Prev = Ha_{(FI \# FE = HL)} + Sr + Fb + Ag$	561.26	3.54	0.05	0.17	551.11	5	0.05
$Prev = Ha_{(FI \# FE = HL)} + Ag$	561.47	3.76	0.04	0.15	555.41	3	4.36
$Prev = Ha_{(FI = FE \# HL)} + Sr + Fb + Ag$	561.75	4.03	0.04	0.13	551.60	5	0.55
Prev = Sr + Ag	562.27	4.55	0.03	0.10	556.21	3	5.15
$Prev = Ha_{(FI = FE \# HL)} + Ag$	562.41	4.69	0.03	0.10	556.35	3	5.30
Prev = Fb	563.12	5.40	0.02	0.07	559.09	2	8.04
$Prev = Ha_{(FI \# FE = HL)} + Sr + Ag$	563.24	5.53	0.02	0.06	555.15	4	4.09
$Prev = Ha_{(FI \# FE \# HL)} + Sr + Fb + Ag$	563.26	5.55	0.02	0.06	551.06	6	0.00
$Prev = Ha_{(FI \# FE \# HL)} + Ag$	563.51	5.79	0.01	0.06	555.41	4	4.35
$Prev = Ha_{(FI = FE \# HL)} + Sr + Ag$	564.17	6.45	0.01	0.04	556.07	4	5.02
$Prev = Ha_{(FI \# FE = HL)} + Fb$	564.68	6.96	0.01	0.03	558.62	3	7.57
$Prev = Ha_{(FI = FE \# HL)} + Fb$	564.71	6.99	0.01	0.03	558.65	3	7.59
Prev = Sr + Fb	565.03	7.31	0.01	0.03	558.97	3	7.92
$Prev = Ha_{(FI \# FE \# HL)} + Sr + Ag$	565.24	7.53	0.01	0.02	555.10	5	4.04
$Prev = Ha_{(FI = FE \# HL)} + Sr + Fb$	566.45	8.74	0.00	0.01	558.36	4	7.30
$Prev = Ha_{(FI \# FE = HL)} + Sr + Fb$	<u>566.5</u> 3	8.81	0.00	0.01	558.43	4	7.38
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			table continued					
Model	AICc <b>AAIC</b> c	w <sub>i</sub>	L	-2LogL	K	D		
$Prev = Ha_{(FI \# FE \# HL)} + Fb$	566.59 8.87	0.00	0.01	558.49	4	7.44		
Prev = Intercept only	567.57 9.85	0.00	0.01	565.56	1	14.50		
$Prev = Ha_{(FI \# FE = HL)}$	568.31 10.59	0.00	0.01	564.28	2	13.23		
$Prev = Ha_{(FI \# FE \# HL)} + Sr + Fb$	568.35 10.64	0.00	0.00	558.21	5	7.15		
$Prev = Ha_{(FI = FE \# HL)}$	568.40 10.69	0.00	0.00	564.38	2	13.32		
Prev = Sr	569.51 11.79	0.00	0.00	565.48	2	14.42		
$Prev = Ha_{(FI \# FE \# HL)}$	570.02 12.30	0.00	0.00	563.96	3	12.90		
$Prev = Ha_{(FI \# FE = HL)} + Sr$	570.33 12.61	0.00	0.00	564.27	3	13.22		
$Prev = Ha_{(FI = FE \# HL)} + Sr$	570.43 12.72	0.00	0.00	564.37	3	13.32		
$Prev = Ha_{(FI \# FE \# HL)} + Sr$	572.06 14.34	0.00	0.00	563.96	4	12.90		



Figure 4.1. Avian malaria sample prevalence in birds collected in Cuc Phuong National Park in summer 2007. 95% confidence intervals are shown. The pattern of prevalence in birds collected in Tam Dao National Park is similar.

#### **CHAPTER 5**

# AVIAN INFLUENZA VIRUS IN WILD LAND BIRDS IN NORTHERN VIETNAM

Abstract: Avian influenza (AI) viruses are currently considered one of the most important bird-associated groups of zoonotic pathogens. However, little information is available about the occurrence of AI viruses in land birds, especially in Southeast Asia including Vietnam, an area that is experiencing a relatively high incidence of outbreaks in humans and domestic poultry. To begin to fill this information gap, my study focused on surveillance for the presence of AI virus nucleic acids and antibodies for AI viruses in free-ranging wild land birds in northern Vietnam. In 2007, serum samples were collected from 197 birds. Serum samples from four birds including Black-crested Bulbul (Pycnonotus melanicterus), Crow-billed Drongo (Dicrurus annectans), Buff-breasted Babbler (*Pellorneum tickelli*), and Black-browed Fulvetta (*Alcippe grotei*) were antibody positive for the H5 subtype. In 2008, tracheal and cloacal swab samples were collected from 193 birds. Using the rRT-PCR test (without virus isolation), nine tracheal swab samples and one cloacal swab sample collected from 10 Japanese White-eyes (Zosterops *japonicus*) were positive for the influenza A virus M gene. Additionally, tracheal swab samples collected from other two Puff-throated Bulbuls (Alophoixus pallidus) tested

positive. Following virus isolation, one tracheal swab sample collected from a Whitetailed Robin (Cinclidium leucurum) and one tracheal swab sample collected from a Striped Tit Babbler (*Macronous gularis*) were positive for the viral M gene by rRT-PCR. Using both methods, 12 samples were positive for AI virus RNA and two were positive for viable AI virus, producing a sample prevalence of 7.25%. Tracheal swab samples make up 92.86% of positive sample and cloacal swab samples make up only 7.14% of positive samples, using both tests. Almost all positive samples were from birds that forage in flocks. Japanese White-eyes had an unusually high prevalence of 14.93%. This result suggests that attention should be given to land birds in AI surveillance and monitoring programs. Among land birds, special attention should be given to the social, flocking species due to their higher AI prevalence compared to other groups. In particular, Japanese White-eyes may be an effective focal species in AI virus surveillance or monitoring programs in Southeast Asia. Both types of swab samples, tracheal (or oropharyngeal) and cloacal, should be collected and processed if both HPAI and LPAI virus detection is of interest. Lastly, more studies should focus on the link between the incidence of outbreaks of HPAI in domestic poultry and the presence of HPAI viruses in land birds close to the outbreak sites.

## **INTRODUCTION**

Much attention has been given to avian diseases recently due to increasing concerns over human and animal health, economic losses due to disease in birds, and biodiversity conservation (Daszak et al. 2004). Many wild birds serve as reservoirs of pathogens and can facilitate the transmission of pathogens among wildlife, human, and domestic animal populations (Chen et al. 2005, Gilchrist 2005, Kilpatrick et al. 2006, Normile 2006, Olsen et al. 2006). Beyond the human health and argriculture concerns, increasing evidence suggests that disease has adverse impacts on wild bird populations (Daszak et al. 2004, Smith et al. 2006). To date, infectious diseases have caused the extinction of 31 animal species, of which 18 are avian species (Smith et al. 2006). The IUCN Red List includes 223 animal species listed as 'critically endangered' with infectious diseases as a contributing factor (Smith et al. 2006).

Avian influenza (AI) viruses are currently considered one of the most important bird-associated groups of zoonotic pathogens. This is in large part because of the attention drawn to birds from the high levels of culling and disease-associated mortality resulting from recent outbreaks of highly pathogenic avian influenza (HPAI) viruses of the H5N1 subtype. Avian influenza viruses, which are all type A influenza viruses, are named according to the hemagglutinin (H1-H16) and neuraminidase (N1-N9) glycoproteins found on the surface of the virus (Spackman 2008). All viral subtypes have been isolated from wild birds (Alexander 2000). Overall, AI viruses have been detected in at least 105 different wild bird species, belonging to 26 families (Olsen et al. 2006). The death of aproximately 1300 Common Terns (*Sterna hirundo*) in South Africa in 1961, due to a HPAI H5N3 virus, was the first AI-induced mortality case

recorded in wildlife (Becker 1966). Almost all HPAI viruses are in the H5 and H7 subtypes (Alexander 2007a) of which HPAI H5N1 virus was recently implicated in outbreaks in domestic poultry in many regions of Eurasia and Africa (Alexander and Capua 2008). HPAI H5N1 has been implicated as the cause of mortality in a variety of wild bird species (Ellis et al. 2004, Kelly et al. 2008, Khan et al. 2009, Zhou et al. 2006). HPAI H5N1 has also killed wild mammals in captivity (Amonsin et al. 2006, Keawcharoen et al. 2004, Roberton et al. 2006) and has been responsible for illness and substantial mortality in humans, including 110 human cases in Vietnam, resulting in the deaths of 55 people (WHO 2009).

Due to the roles wild birds may play as reservoirs or as transmission bridges between organisms, and because they are directly threatened by HPAI H5N1, many wild bird populations have been surveyed for AI viruses globally (e.g.,Gaidet et al. 2007, Iverson et al. 2008, Lei et al. 2007). While AI viruses in general, and HPAI H5N1 in particular, have been detected in wild birds, most affected species inhabit wetlands or aquatic habitats (Olsen et al. 2006, Stallknecht and Brown 2007) such that land bird species are not currently considered important reservoirs of HPAI H5N1. Emerging evidence indicates that land birds could play an important role in preserving and circulating HPAI H5N1 in the enviroment (Gronesova et al. 2008, Kou et al. 2005, Peterson et al. 2008). However, little information is available about the occurrence of AI viruses in land birds, especially in Southeast Asia including Vietnam, an area that is experiencing a relatively high incidence of outbreaks in humans and domestic poultry (Alexander 2007b, Hien et al. 2009). To begin to fill this information gap, my study focused on surveillance for the presence of AI virus nucleic acids and antibodies for AI viruses in free-ranging wild land birds in northern Vietnam. My study also sets the stage to investigate potential biological and ecological factors that regulate the presence of AI viruses in forest ecosystems.

# **METHODS**

## Study areas

The research was conducted in and near Cuc Phuong National Park (CPNP; 20°  $14' - 20^{\circ} 24' \text{ N}$ ;  $105^{\circ} 29' - 105^{\circ} 44' \text{ E}$ ; Appendix I) and Tam Dao National Park (TDNP;  $21^{\circ} 21' - 21^{\circ} 42'$  N;  $105^{\circ} 23' - 105^{\circ} 44'$  E; Appendix I) in northern Vietnam. The study areas in the parks were comprised of mature and regrowth forests and were located at or below 300m in elevation. The two parks have a tropical climate with two distinctive seasons driven by monsoon winds. The hot and rainy season extends from April to November while the cool and dry season is from December through March. The parks are surrounded by rural areas and many people living near the parks rely on farming and small domestic fowl operations for subsistence. These sorts of backyard poultry and duck flocks are free-ranging and can range in size from dozens to hundreds of birds. Ducks feed in rice fields, agricultural channels, or rivers where migrating wild water birds have also been observed (Vu, pers. obs.). These domestic fowl can be infected from, or can infect migratory birds with, disease pathogens such as AI viruses that persist in some water environments (Stallknecht et al. 1990). Resident land birds can also be infected with pathogens from domestic fowl or migratory birds and thus become natural reservoirs of AI viruses in the region.

## Sample collection

Samples were collected from wild birds in June and July 2007 and July 2008 in the two National Parks in northern Vietnam. I captured birds using mist nets in three habitat types including forest interior, forest edge, and human-dominated landscapes. Sample sizes were determined by time available in the field, laboratory processing capacity, and permission to access the land. Birds were aged as 'juvenile' or 'adult' based on feather characteristics and classified to species following Robson (2005). In 2007, serum samples were collected from birds at CPNP. I collected less than 10% of total blood volume from each bird via jugular venipuncture. Captured birds weighing less than 12g were not sampled. Blood was placed in serum separator tubes (Becton Dickinson, Franklin Lakes, NJ, USA), centrifuged in a portable centrifuge to separate out the serum, and the sera were then transferred to cryotubes and frozen at -20°C until shipped for subsequent processing. In 2008, cloacal and tracheal swab samples were collected from birds captured at TDNP. One cloacal and one tracheal swab sample were collected from each bird and stored in cryogenic vials containing Viral Transport Medium (WHO 2006). Swab samples were stored at -80°C before shipping for subsequent processing.

# Sample processing

Serum samples collected in 2007 were processed at the Department of Virology, Institute of Animal Health, Hanoi, Vietnam. Subtype-specific antibodies were detected using the hemagglutination inhibition (HI) test (Pedersen 2008). Seven different HI tests, specific for antibodies against H3, H4, H5, H6, H7, H9, and H11 hemagluttinin subtypes were run for each sample. Cloacal and tracheal swabs collected in 2008 were processed at the Veterinary Diagnostic Laboratory, Department of Veterinary Science, Chulalongkorn University, Bangkok, Thailand. Aliquots from samples of the same type and same species were pooled (up to five samples pooled together) and the remainder of the original samples was preserved in RNA Later (Ambion, Applied Biosystems, Austin, TX, USA) and stored at -80°C for future analysis as needed. Aliquots from the pooled samples were then assayed for two different targets: a) to detect the presence of AI viral nucleic acids (RNA) and b) to detect viable virus by virus isolation.

Aliquots of the pooled samples were screened for the presence of viral nucleic acids using real-time reverse transcriptase-polymerase chain reaction (rRT-PCR) directed at the conserved viral matrix gene (M gene; Spackman et al. 2002). If the pooled samples were positive in the initial test, subsequent tests using the same rRT-PCR protocol were performed on each of the individual samples in the pool to identify the specific samples that were positive for AI virus RNA. I considered Ct values < 40 as 'positive'.

Aliquots of pooled samples were also inoculated in embryonated chicken eggs for virus isolation (Woolcock 2008). After two passages, a sample of the allantoic fluid was then subjected to a hemagglutination assay (HA) to confirm the presence of virus and not another agent in the egg inoculum (Killian 2008). For HA-positive samples, rRT-PCR directed at the M gene (Spackman et al. 2002) was subsequently carried out to confirm the presence of an influenza A virus.

## RESULTS

In 2007, 197 free-ranging birds from 45 species representing 15 families were captured in CPNP (Appendix IV). Serum samples from four birds including Black-crested Bulbul (*Pycnonotus melanicterus*), Crow-billed Drongo (*Dicrurus annectans*), Buff-breasted Babbler (*Pellorneum tickelli*), and Black-browed Fulvetta (*Alcippe grotei*) were antibody positive for the H5 subtype. Of these four birds, one was also antibody positive for the H6 subtype. Additionally, a Red-whiskered Bulbul (*Pycnonotus jocosus*) was antibody positive for the H9 subtype. No samples tested positive for H3, H4, H7, or H11 subtypes.

In 2008, 193 free-ranging birds from 24 species representing 11 families were captured in TDNP (Appendix V). Using the rRT-PCR test (without virus isolation), nine tracheal swab samples and one cloacal swab sample collected from 10 Japanese White-eyes (*Zosterops japonicus*) were positive for the viral M gene (Table 5.1). Additionally, tracheal swab samples collected from another two Puff-throated Bulbuls (*Alophoixus pallidus*) tested positive. Following virus isolation, one tracheal swab sample collected from a White-tailed Robin (*Cinclidium leucurum*) and one tracheal swab sample collected from a Striped Tit Babbler (*Macronous gularis*) were positive for the viral M gene by rRT-PCR (Table 5.2). Using both methods, 12 samples were positive for AI virus RNA and two were positive for viable AI virus, producing a sample prevalence of 7.25%. Tracheal swab samples make up 92.86% (13 of 14) of positive samples, using both tests.

## DISCUSSION

Serum samples from four birds captured at CPNP had antibodies specific to the H5 avian influenza virus subtype. Although the neuraminidase subtype was not determined, this result suggests a potential link to the incidences of outbreaks of HPAI H5N1 in domestic poultry in the human-dominated areas surrounding CPNP in the spring of 2007 and in civets right within the Park in 2006 (Roberton et al. 2006) and 2008 (Vietnam Department of Animal Health 2009). Some evidence exists suggesting that HPAI H5N1 has killed some land bird species (Khan et al. 2009, Li et al. 2004, Mase et al. 2005). However, HPAI H5N1 viruses have also been isolated from live land birds exhibiting typical behavior and normal health at capture in China (Kou et al. 2005). This suggests that some land bird species can produce antibodies against HPAI viruses and subsequently survive the infection. The detection of antibodies against H5 subtype in my study strengthens this hypothesis. By surviving the infection, land birds can play a role as a reservoir and circulate the AI viruses in the environment as they move locally to forage. Therefore, infected wild land birds could be long-term carriers of the viruses and thus serve as sources of infection to other wild land birds, water birds, and domestic poultry.

In 2008, sample prevalence for the presence of virus was 7.25% using both methods to detect virus RNA and viable virus in swab samples. This value is higher than the prevalence reported in a recent study conducted in Southeast China (24 of 939 samples or 2.3%), relatively geographically close to northern Vietnam (Peterson et al. 2008). Peterson et al. (2008) used only cloacal swab samples and did not conduct virus isolation, therefore, their sample prevalence could be an underestimate. These results, together with some recent studies that found a surprisingly high prevalence of AI viruses

in land birds (Gronesova et al. 2008, Kou et al. 2005), support the idea that land birds can be effective reservoirs of AI viruses.

Sociality is believed to enhance the transmission of disease pathogens among animals (Coté and Poulin 1995, Dobson 1988, Freeland 1976) in part because parasite transmission is usually density-dependent (Anderson and May 1979, Mccallum et al. 2001). Four out of five of the birds captured at CPNP that were detected to have antibodies against AI viruses forage in flocks. Similarly, 13 out of 14 of the birds captured at TDNP that tested 'positive' forage in flocks. Flocks of Red-whiskered Bulbul, Black-crested Bulbul, or Japanese White-eye can have dozens of individuals. In the tropics, these species can also join mixed-species flocks that can contain many individuals of several species during the non-breeding season (Lee et al. 2005) when birds are likely to be roosting or moving locally together. Flocking behaviors might enhance the transmission of pathogens among birds due to frequent social interactions, such as food sharing, using the same food or water sources, or allogrooming thus leading to higher prevalence in flocking birds.

Among the flocking species, Japanese White-eyes show the highest sample prevalence. If this species is considered alone, AI virus prevalence is 14.93%. Given relatively high sample prevalences and that they are abundant and easy to capture, the Japanese White-eye could be a useful focal species for AI virus surveillance or monitoring programs. The Japanese white-eye typically lives in close contact with humans (65 and two of the white-eyes caught in this study were in the human-dominated landscape and forest edge, respectively) leading to potentially increased interactions with domestic poultry and AI virus transmission through shared resources or other
interactions. The Japanese White-eye has a broad geographic range, distributed in most parts of East and Southeast Asia, where most of the current outbreaks of the HPAI H5N1 virus has been recorded. Using the same focal species could enhance data comparisons about AI viruses among regions of Asia as well as serve as a sentinel species for the detection of emerging outbreaks.

Apart from the results in Japanese White-eyes, habitat type does not seem to be tightly linked with the presence of AI virus in sampled birds because positive birds were equally distributed among habitats. Samples were taken in June and July when migratory birds are not present. Possible transmission of AI between land birds and migratory water birds might happen, instead, during the winter. Virus in land birds surviving AI infection can then be eliminated or diminished to undetectable levels and disease symptoms become latent. Similarly, after eliminating the virus, antibodies might diminish to undetectable levels. These factors might account for the similarity between prevalence of AI virus in different habitat types recorded in this study in the summer. Understanding how AI viruses are distributed among habitats and how migratory water birds and domestic poultry affect the prevalence of AI in land birds are interesting areas that require additional research, particularly in the winter.

For the swab samples taken from birds at TDNP in 2008, only 0.52% of cloacal samples tested 'positive' for AI viruses, much lower than the 6.77% of tracheal swab samples. Using both methods, tracheal swab samples make up 92.86% of positive samples and cloacal swab samples make up only 7.14% of positive samples. Using only cloacal swab samples for processing may lower the chance of detecting currently or previously infected or exposed birds and lead to underestimates of prevalence. In wild

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birds, low pathogenic avian influenza (LPAI) viruses are replicated in tissues in the gastrointestinal tract and virus is shed in the feces so cloacal swab samples should be collected for detection of these viruses (Brown and Stallknecht 2008). In contrast, oropharyngeal or tracheal swab samples should be collected from wild birds for testing for HPAI H5N1 type viruses because wild birds primarily shed H5N1 viruses through the oropharyngeal or respiratory route (Brown and Stallknecht 2008). My study has not classified the AI viruses to specific subtypes, however, a study that is geographically close to my study reported that 2.3% of sampled birds carried AI viruses other than H5 subtypes (Peterson et al. 2008) suggesting that some of the infected birds in my study may actually carry LPAIs. On the other hand, that 92.86% of the 'positive' samples collected from TDNP in 2008 were tracheal samples supports the idea that HPAI H5N1viruses might be present in wild land birds in northern Vietnam. HPAI viruses are more likely to be detected in tracheal rather than cloacal swab samples because HPAI virus shedding is of longer duration and higher titer tracheally compared to cloacal shedding (Brown et al. 2006). Therefore, for surveillance of AI in land birds, I suggest collecting and processing both types of samples including tracheal (or oropharyngeal) and cloacal swabs for AI virus detection.

In conclusion, more attention should be given to land birds in AI surveillance and monitoring programs due to the role land birds may play in the circulation of AI viruses and the paucity of AI virus surveillance data on them. Active surveillance of live birds should be used along with dead bird surveillance because infected birds can survive the infection and become long-term living carriers of the virus. Among land birds, special attention should be given to the social, flocking species. In particular, Japanese Whiteeyes may be an effective focal species in AI virus surveillance or monitoring programs in Southeast Asia. Both types of swab samples, tracheal (or oropharyngeal) and cloacal, should be collected and processed if both HPAI and LPAI virus detection is of interest. In the case of resource limitation, tracheal swab samples should be a priority. Lastly, more studies should focus on the link between the incidence of outbreaks of HPAI in domestic poultry and the presence of HPAI viruses in land birds close to the outbreak sites.

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Table 5.1. Test results for positive samples using real time RT-PCR directed at the viral M gene on cloacal swab and tracheal swab samples collected from birds sampled in Tam Dao National Park, Vietnam in 2008.

Common name	Scientific Name	Sample type	Ct value
Japanese White-eye	Zosterops japonicus	Tracheal swab	35.68
Japanese White-eye	Zosterops japonicus	Tracheal swab	39.37
Japanese White-eye	Zosterops japonicus	Tracheal swab	39.51
Japanese White-eye	Zosterops japonicus	Tracheal swab	37.86
Japanese White-eye	Zosterops japonicus	Tracheal swab	38.37
Japanese White-eye	Zosterops japonicus	Tracheal swab	38.81
Japanese White-eye	Zosterops japonicus	Tracheal swab	36.93
Japanese White-eye	Zosterops japonicus	Tracheal swab	39.92
Japanese White-eye	Zosterops japonicus	Tracheal swab	34.68
Japanese White-eye	Zosterops japonicus	Tracheal swab	31.60
Puff-throated Bulbul	Alophoixus pallidus	Tracheal swab	37.30
Puff-throated Bulbul	Alophoixus pallidus	Tracheal swab	37.52

Table 5.2. Test results for positive samples using virus isolation followed by Real-time RT-PCR with M gene on allantoic fluid collected from birds sampled in Tam Dao National Park, Vietnam in 2008.

Common name	Scientific Name	Sample type	Ct value
White-tail Robin	Myiomela leucura	Tracheal swab	35.00
Striped Tit Babbler	Macronous gularis	Tracheal swab	39.07

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Appendix I. Locations of study areas

English name	Scientific name	MF	SG	PP	bo (cm)	co	si
Phasianidae	Phasianidae						
Red Junglefowl	Gallus gallus		Х	х	62.0	3	1
Picidae	Picidae						
White-browed Piculet	Sasia ochracea	х	Х	х	9.0	3	0
Grey-capped Woodpecker	Dendrocopus canicapillus	х			14.0	4	0
Lesser Yellownape	Picus chlorolophus	х			27.0	1	0
Greater Yellownape	Picus flavinucha	х			33.0	4	1
Grey-faced Woodpecker	Picus canus			х	32.5	1	0
Greater Flameback	Chrysocolaptes lucidus	х			32.0	1	0
Bay Woodpecker	Blythipicus pyrrhotis	х			28.0	5	1
Megalaimidae	Megalaimidae						
Great Barbet	Megalaima viren	х			32.5	1	1
Red-vented Barbet	Megalaima lagrandieri	х	х	x	32.0	5	1
Green-eared Barbet	Megalaima faiostricta	х	х	х	26.0	5	1
Golden-throated Barbet	Megalaima franklinii	х	х		22.0	1	1
Trogonidae	Trogonidae						
Red-headed Trogon	Harpactes erythrocephalus	х	х		33.0	5	1
Alcedinidae	Alcedinidae						
Common Kingfisher	Alcedo atthis	х			17.0	1	0
Cuculidae	Cuculidae						
Indian Cuckoo	Cuculus micropterus			х	32.0	2	1
Chestnut-winged Cuckoo	Clamator coromandus			х	40.0	4	1
Green-billed Malkoha	Phaenicophaeus tristis	х	х	х	56.0	3	1
Centropodidae	Centropodidae						
Greater Coucal	Centropus sinensis		х	х	50.0	1	1
Strigidae	Strigidae						
Collared Scops-Owl	Otus bakkamoena	х	х		23.0	3	1
Collared Owlet	Glaucidium brodiei		х		16.5	5	1
Columbidae	Columbidae						
Spotted Dove	Streptopelia chinensis			x	30.5	4	1
Emerald Dove	Chalcophaps indica	х	х		25.0	3	1

Appendix II. List of species detected in three habitat types during the surveys in summer 2006 in Tam Dao National Park with covariates (MF=mature forest, SG=Secondary growth forest, PP=Pine plantation, bo=body length, co=regional commonness index<sup>1</sup>, and si=singing propensity<sup>2</sup>).

English name	Scientific name	MF	SG	PP	bo	co	si
Pittidae	Pittidae				`		
Blue-rumped Pitta	Pitta soror	х	х		21.0	1	1
Eurylaimidae	Eurylaimidae						
Long-tailed Broadbill	Psarisomus dalhousiae	Х			26.0	4	1
Silver-breasted Broadbill	Serilophus lunatus	Х	х		17.0	4	1
Laniidae	Laniidae						
Long-tailed Shrike	Lanius schach			x	26.5	4	1
Corvidae	Corvidae						
Blue Magpie	Urocissa erythrorhyncha			x	67.0	4	1
Green Magpie	Cissa chinensis	Х			39.0	3	1
Indochinese Green Magpie	Cissa hypoleuca	Х		х	33.0	3	0
Grey Treepie	Dendrocitta formosae	Х	х	х	38.0	1	1
Scarlet Minivet	Pericrocotus flammeus	х			19.0	5	1
White-throated Fantail	Rhipidura albicollis	х		х	19.0	1	1
Bronzed Drongo	Dicrurus aeneus	х	х		23.0	3	1
Lesser Racket-tailed Drongo	Dicrurus remifer	х			33.5	1	0
Ashy Drongo	Dicrurus leucophaeus			x	27.0	5	0
Crow-billed Drongo	Dicrurus annectans	х			29.5	5	0
Black-naped Monarch	Hypothymis azurea	Х	х	x	16.5	5	1
Asian Paradise-Flycatcher	Terpsiphone paradisi	Х	х	x	21.0	5	1
Muscicapidae	Muscicapidae						
Orange-headed Thrush	Zoothera citrina	х			22.0	3	0
Scaly Thrush	Zoothera dauma	Х	х		28.5	1	1
White-throat Rock Thrush	Monticola gularis	Х			22.5	1	0
Vivid Niltava	Niltava grandis	Х			20.5	1	0
White-tailed Flycatcher	Cyornis concretus	Х			19.0	4	1
Grey-headed Canary-Flycatcher	Culicicapa ceylonensis	Х			12.0	4	1
Oriental Magpie-Robin	Copsychus saularis		х		20.0	1	1
White-tailed Robin	Myiomela leucura	х			18.5	1	1
Green Cochoa	Cochoa viridis	х			28.0	2	1
Sturnidae	Sturnidae						
Crested Myna	Acridotheres cristatellus		х		26.5	1	1
Paridae	Paridae						
Great Tit	Parus major		х	x	14.0	5	1
Sultan Tit	Melanochlora sultanea	Х			20.5	5	1
Pycnonotidae	Pycnonotidae						
Black-crested Bulbul	Pycnonotus melanicterus	х	х		19.0	3	0

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English name	Scientific name	MF	SG	РР	bo (cm)	co	si
Red-whiskered Bulbul	Pycnonotus jocosus		х	х	19.0	5	1
Sooty-headed Bulbul	Pycnonotus aurigaster	х	х	х	20.0	1	1
Puff-throated Bulbul	Alophoixus pallidus	х	х	х	23.5	5	1
Grey-eyed Bulbul	Iole propinqua	х	х		18.0	4	1
Chestnut Bulbul	Hemixos castanonotus	х			21.5	5	1
Mountain Bulbul	Hypsipetes mcclellandii		х		23.5	1	1
Priniidae	Priniidae						
Rufescent Prinia	Prinia rufescens		х	х	11.5	4	0
Zosteropidae	Zosteropidae						
Japanese White-eye	Zosterops japonicus		х		10.5	1	1
Sylviidae	Sylviidae						
Pale-footed Bush-Warbler	Cettia pallidipes			х	11.5	1	0
Common Tailorbird	Orthotomus sutorius		х	х	12.0	5	1
Dark-necked Tailorbird	Orthotomus atrogularis	х	х	х	11.0	4	0
Yellow-bellied Warbler	Abroscopus superciliaris	х	х		10.5	4	0
Masked Laughingthrush	Garrulax perspicillatus		х		31.0	4	0
White-crested Laughingthrush	Garrulax leucolophus	х		х	29.0	1	1
Lesser Necklaced Laughingthrush	Garrulax monileger	х	х	х	29.0	4	1
Greater Necklaced Laughingthrush	Garrulax pectoralis	х		х	31.0	4	0
Grey Laughingthrush	Garrulax maesi	х			29.0	5	1
Black-throated Laughingthrush	Garrulax chinensis		х	х	28.0	4	1
Hwamei	Garrulax canorus		х		23.0	4	1
Buff-breasted Babbler	Pellorneum tickelli	х	х	х	14.5	5	1
Spot-throated Babbler	Pellorneum albiventre	х			13.5	1	0
Puff-throated Babbler	Pellorneum ruficeps	Х	х	х	17.0	3	1
Large Scimitar-Babbler	Pomatorhinus hypoleucos	х	х	х	27.0	4	1
Streak-breasted Scimitar-Babbler	Pomatorhinus ruficollis	х	х	х	18.0	3	1
Red-billed Scimitar-Babbler	Pomatorhinus ochraceiceps	Х	х	х	23.0	1	1
Streaked Wren-Babbler	Napothera brevicaudata	Х	х		14.0	4	0
Eye-browed Wren-Babbler	Napothera epilepidota	Х	х		10.5	4	1
Rufous-capped Babbler	Stachyris ruficeps	Х	х		12.5	1	0
Golden Babbler	Stachyris chrysaea	Х	х	х	11.0	5	1
Grey-throated Babbler	Stachyris nigriceps	Х	х	х	13.0	5	1
Spot-necked Babbler	Stachyris striolata	х	х	х	16.0	5	1
Striped Tit-Babbler	Macronous gularis	Х	х	х	13.0	5	1
Silver-eared Mesia	Leiothrix argentauris		х		17.0	3	1
White-browed Shrike-Babbler	Pteruthius flaviscapis	х			16.5	1	1

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English name	Scientific name	MF	SG	PP	bo (cm)	co	si
White-hooded Babbler	Gampsorhynchus rufulus	х	х	х	25.0	5	1
Rufous-throated Fulvetta	Alcippe rufogularis	х	х		13.0	1	1
Grey-cheeked Fulvetta	Alcippe morrisonia	х	х	х	14.0	5	1
Black-chinned Yuhina	Yuhina nigrimenta		х		13.0	4	1
White-bellied Yuhina	Yuhina zantholeuca	х	х	х	12.5	5	1
Nectariniidae	Nectariniidae						
Yellow-bellied Flowerpecker	Dicaeum concolor		х		8.5	1	0
Olive-backed Sunbird	Nectarinia jugularis		х	х	11.5	1	0
Fork-tailed Sunbird	Aethopyga christinae	х	х	х	11.0	5	1
Black-throated Sunbird	Aethopyga saturata	х	х	х	13.0	3	1
Crimson Sunbird	Aethopyga siparaja	Х	х		12.0	3	1
Little Spiderhunter	Arachnothera longirostra	х			16.0	1	0
Streaked Spiderhunter	Arachnothera magna	Х			18.5	4	1
Passeridae	Passeridae						
White-rumped Munia	Lonchura striata		х		11.0	4	0

<sup>1</sup> Regional commonness index was scored according to 5 categories of abundance: common - 5, fairly common - 4, uncommon-3, scare - 2, rare - 1. Scoring was inferred from Davison et al. (2005), Robson (2005), and Cu et al. (2000) and prior experience. <sup>2</sup> Species that can be recognized easily during the survey by their typical calls or songs and tend to sing often are assigned the value 1 for singing propensity, the others are assigned a 0.

English name	Scientific name	Number of birds	Number of infected birds
Picidae	Picidae		
White-browed Piculet	Sasia ochracea	5	0
Rufous-bellied Woodpecker	Dendrocopus hyperythrus	1	1
Alcedinidae	Alcedinidae		
Common Kingfisher	Alcedo atthis	18	4
Black-backed Kingfisher	Ceyx erithacus	1	0
Columbidae	Columbidae		
Emerald Dove	Chalcophaps indica	1	0
Meropidae	Meropidae		
Blue-bearded Bee-eater	Nyctyornis athertoni	1	1
Pittidae	Pittidae		
Bar-bellied Pitta	Pitta elliotii	1	0
Laniidae	Laniidae		
Long-tailed Shrike	Lanius schach	2	2
Chloropseidae	Chloropseidae		
Blue-winged Leafbird	Chloropsis cochinchinenss	1	1
Corvidae	Corvidae		
Indochinese Green Magpie	Cissa hypoleuca	1	1
Racket-tailed Treepie	Crypsirina temia	1	1
Crow-billed Drongo	Dicrurus annectans	8	2
Black-naped Monarch	Hypothymis azurea	19	8
Bar-winged Flycatcher-shrike	Hemipus picatus	6	6
Asian Paradise-Flycatcher	Terpsiphone paradisi	2	1
Common Iora	Aegithina tiphia	10	3
Large Woodshrike	Tephrodornis gularis	6	2
Muscicapidae	Muscicapidae		
Hainan Blue-Flycatcher	Cyornis hainanus	1	1
Snowy-browed Flycatcher	Ficedula hyperythra	2	0
Small Niltava	Niltava macgrigoriae	1	1
Vivid Niltava	Niltava vivida	2	1
Blue-throated Flycatcher	Cyornis rubeculoides	1	0
Red-flanked Bluetail	Tarsiger cyanurus	7	3
Oriental Magpie-Robin	Copsychus saularis	7	6
		appendix continu appendix continu	
English name	Scientific name	Number of birds	Number of infected birds

Appendix III. List of birds with molecular screening for avian malarial parasites sampled in Cuc Phuong and Tam Dao National Parks in summer 2007 and 2008.

Slaty-backed Forktail	Enicurus schistaceus	2	0
White-tailed Robin	Cinclidium leucurum	2	0
Paridae	Paridae		
Great Tit	Parus major	16	5
Pycnonotidae	Pycnonotidae		
Black-crested Bulbul	Pycnonotus melanicterus	8	5
Red-whiskered Bulbul	Pycnonotus jocosus	47	29
Sooty-headed Bulbul	Pycnonotus aurigaster	11	8
Stripe-throated Bulbul	Pycnonotus finlaysoni	5	3
Light-vented Bulbul	Pycnonotus sinensis	2	2
Puff-throated Bulbul	Alophoixus pallidus	16	6
Grey-eyed Bulbul	Iole propinqua	4	4
Zosteropidae	Zosteropidae		
Japanese White-eye	Zosterops japonicus	71	43
Sylviidae	Sylviidae		
Common Tailorbird	Orthotomus sutorius	2	1
Buff-breasted Babbler	Pellorneum tickelli	24	6
Puff-throated Babbler	Pellorneum ruficeps	8	1
Large Scimitar-Babbler	Pomatorhinus hypoleucos	1	1
Streak-breasted Scimitar-Babbler	Pomatorhinus ruficollis	2	0
Grey-throated Babbler	Stachyris nigriceps	13	5
Spot-necked Babbler	Stachyris striolata	8	7
Scaly-crowned Babbler	Malacopteron cinereum	2	1
Chestnut-capped Babbler	Timalia pileata	6	3
Limestone Wren-Babbler	Napothera crispifrons	1	0
Rufous-throated Fulvetta	Alcippe rufogularis	4	3
Black-browed Fulvetta	Alcippe grotei	14	7
Grey-cheecked Fulveta	Alcippe morrisonia	7	2
Striped Tit-Babbler	Macronous gularis	16	6
White-bellied Yuhina	Yuhina castaniceps	2	0

		pendix continued	
English name	Scientific name	Number of birds	Number of infected birds
Nectariniidae	Nectariniidae		
Fork-tailed Sunbird	Aethopyga christinae	1	1
Crimson Sunbird	Aethopyga siparaja	1	1
Olive-backed Sunbird	Arachnothera jugularis	2	1
Little Spiderhunter	Arachnothera longirostra	1	1
Purple-naped Sunbird	Hypogramma hypogammicum	1	1
Passeridae	Passeridae		
Scaly-breasted Munia	Lonchura punctulata	6	3
Eurasian Tree Sparrow	Passer rutilans	1	1

English name	Scientific name	Number of birds
Picidae	Picidae	
Rufous-bellied Woodpecker	Dendrocopus hyperythrus	1
Trogonidae	Trogonidae	
Red-headed Trogon	Harpactes erythrocephalus	1
Alcedinidae	Alcedinidae	
Common Kingfisher	Alcedo atthis	11
Columbidae	Columbidae	
Emerald Dove	Chalcophaps indica	1
Meropidae	Meropidae	
Blue-bearded Bee-eater	Nyctyornis athertoni	1
Pittidae	Pittidae	
Bar-bellied Pitta	Pitta elliotii	1
Laniidae	Laniidae	
Long-tailed Shrike	Lanius schach	2
Chloropseidae	Chloropseidae	
Blue-winged Leafbird	Chloropsis cochinchinenss	2
Corvidae	Corvidae	
Indochinese Green Magpie	Cissa hypoleuca	1
Racket-tailed Treepie	Crypsirina temia	1
Crow-billed Drongo	Dicrurus annectans	8
Black-naped Monarch	Hypothymis azurea	11
Bar-winged Flycatcher-shrike	Hemipus picatus	1
Common Iora	Aegithina tiphia	8
Asian Paradise-Flycatcher	Terpsiphone 156aradise	2
Large Woodshrike	Tephrodornis gularis	6
Muscicapidae	Muscicapidae	
Hainan Blue-Flycatcher	Cyornis hainanus	1
Snowy-browed Flycatcher	Ficedula hyperythra	1
Small Niltava	Niltava macgrigoriae	1
Red-flanked Bluetail	Tarsiger cyanurus	6
Oriental Magpie-Robin	Copsychus saularis	6
White-tailed Robin	Cinclidium leucurum	1
Paridae	Paridae	
Great Tit	Parus major	2

Appendix IV. List of birds captured for serum samples in Cuc Phuong National Park in June and July 2007.

	apj	pendix continued
English name	Scientific name	Number of birds
Pycnonotidae	Pycnonotidae	
Black-crested Bulbul	Pycnonotus melanicterus	8
Red-whiskered Bulbul	Pycnonotus jocosus	16
Sooty-headed Bulbul	Pycnonotus aurigaster	6
Stripe-throated Bulbul	Pycnonotus finlaysoni	4
Light-vented Bulbul	Pycnonotus sinensis	1
Puff-throated Bulbul	Alophoixus pallidus	6
Grey-eyed Bulbul	Iole propinqua	5
Sylviidae	Sylviidae	
Buff-breasted Babbler	Pellorneum tickelli	14
Puff-throated Babbler	Pellorneum ruficeps	10
Large Scimitar-Babbler	Pomatorhinus hypoleucos	1
Streak-breasted Scimitar-Babbler	Pomatorhinus ruficollis	1
Grey-throated Babbler	Stachyris nigriceps	11
Spot-necked Babbler	Stachyris striolata	2
Scaly-crowned Babbler	Malacopteron cinereum	2
Chestnut-capped Babbler	Timalia pileata	3
Limestone Wren-Babbler	Napothera crispifrons	1
Rufous-throated Fulvetta	Alcippe rufogularis	6
Black-browed Fulvetta	Alcippe grotei	16
Striped Tit-Babbler	Macronous gularis	4
Nectariniidae	Nectariniidae	
Little Spiderhunter	Arachnothera longirostra	1
Passeridae	Passeridae	
Eurasian Tree Sparrow	Passer rutilans	1
Scaly-breasted Munia	Lonchura punctulata	2

English name	Latin name	Cloacal swabs	Tracheal swabs
Picidae	Picidae		
White-browed Piculet	Sasia ochracea	4	4
Alcedinidae	Alcedinidae		
Common Kingfisher	Alcedo atthis	8	8
Muscicapidae	Muscicapidae		
Oriental Magpie-Robin	Copsychus saularis	1	1
White-tailed Robin	Cinclidium leucurum	2	2
Slaty-backed Forktail	Enicurus schistaceus	2	2
Paridae	Paridae		
Great Tit	Parus major	15	15
Pycnonotidae	Pycnonotidae		
Red-whiskered Bulbul	Pycnonotus jocosus	24	24
Sooty-headed Bulbul	Pycnonotus aurigaster	5	5
Stripe-throated Bulbul	Pycnonotus finlaysoni	2	2
Puff-throated Bulbul	Alophoixus pallidus	10	10
Priniidae	Priniidae		
Rufescent Prinia	Prinia rufescens	2	1
Common Tailorbird	Orthotomus sutorius	10	10
Zosteropidae	Zosteropidae		
Japanese White-eye	Zosterops japonicus	66	67
Sylviidae	Sylviidae		
Buff-breasted Babbler	Pellorneum tickelli	10	10
Grey-throated Babbler	Stachyris nigriceps	5	5
Spot-necked Babbler	Stachyris striolata	4	4
Striped Tit Babbler	Macronous gularis	3	3
Grey-cheecked Fulveta	Alcippe morrisonia	7	7
White-bellied Fulveta	Yuhina zantholeuca	2	2
Dicaeidae	Dicaeidae		
Plain Flowerpecker	Dicaeum concolor	3	3
Nectariniidae	Nectariniidae		
Fork-tailed Sunbird	Aethopyga christinae	2	2
Crimson Sunbird	Aethopyga siparaja	2	1
Olive-backed Sunbird	Arachnothera jugularis	2	2
Passeridae	Passeridae		
Scaly-breasted Munia	Lonchura punctulata	1	1

Appendix V. List of birds captured for tracheal and cloacal swab samples in Tam Dao National Park in July 2008.