DISSERTATION

AVIAN CONSERVATION AND ECOLOGY IN NORTHERN VIETNAM

Submitted by

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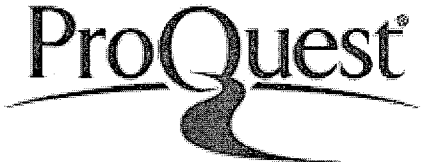

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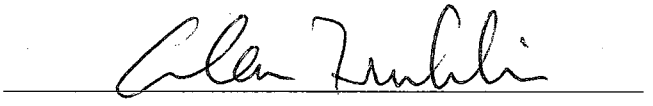

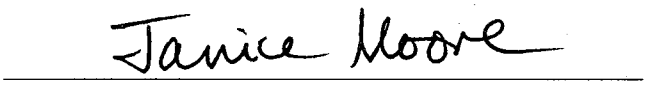

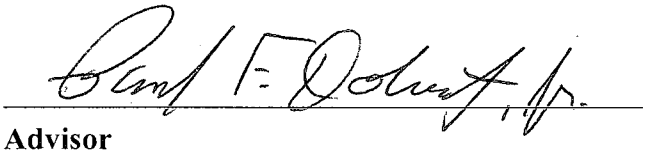

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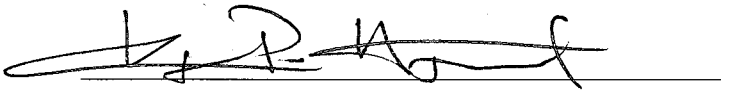

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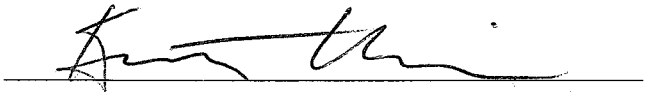

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ABSTRACT OF DISSERTATION

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 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 second-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 (191.36; 95% CI = 95.99, 287.35, and 88.08; 95% CI = 46.94, 129.22 respectively), lower in second-growth (157.92 (95% CI = 87.42, 245.34 and 57.51; 95% CI = 17.51, 97.51 respectively), and lowest in pine plantation (106.02; 95% CI = 52.11, 158.13 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 second-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% CI = 0.72, 0.89 for Buff-breasted Babbler). The response delay time of the mid-canopy

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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 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 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.

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 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

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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 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 considerable 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 Chapter 1 of this dissertation was to examine the avian conservation potential of pine plantations compared to other natural vegetation types including second-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 introduced into forest landscapes raised concern for wildlife conservation in Vietnam. There is evidence that roads can have adverse effects on some wildlife species, 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 increased vegetation heterogeneity, but ultimately some animals inhabiting these environments may have lower survival and/or reproduction such that roads may create habitats that 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 the ability of birds in Southeast Asia to cross gaps 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 Chapter 2, I used playbacks of territorial calls to examine whether forest birds in Southeast Asia are inhibited from crossing roads. 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 some species 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. In Chapter 3, I therefore simulated the effect of different logging schemes on tropical forest biodiversity, relative to birds, and I provided 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, Chapter 4 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, *Plasmodium* and *Haemoproteus,* 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 due to the attention drawn to poultry 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, 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, Chapter 5 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, SECOND-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 was to examine the avian conservation potential of pine plantations relative to other natural vegetation types, such as second-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 three forest types (mature forest, second-growth forest and pine plantation) over six sessions during summer 2006. Bird species were classified into two categories: forest specialists or forest generalists. Number of species in each category was estimated using the Pledger-Huggins estimator with two mixtures to model the large variation in detection probabilities among individual species. Total species richness was estimated by adding these two above estimates. 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 second-growth forest, and lowest in pine plantation. For generalists, detection probability was highest in pine plantation, lower in second-growth forest and least in mature forest. I estimated total species richness and number of forest specialist species to be highest in mature forest (191.36; 95% CI = 95.99, 287.35, and 88.08; 95% CI = 46.94, 129.22 respectively), lower in second-growth (157.92 (95% CI = 87.42, 245.34 and 57.51; 95% CI = 17.51, 97.51 respectively), and lowest in pine plantation (106.02; 95% CI = 52.11, 158.13 and 49.45; 95% CI = 1.84, 97.06 respectively). The estimated number of forest generalist species was similar between mature forest and second-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). Based on these results, 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. 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 low structural complexity because of uniform age and physiognomy of plantation trees and poorly developed understory, which may lead to lower abundance of food items and fewer opportunities for concealment for native birds (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, have potential for conservation of native forest bird species, especially when management practices diversify 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 43% by planting non-native tree plantations. Overall benefits of this plan will be enhanced if conservation values can be balanced with

economic concerns. In this chapter, my objective was to examine the avian conservation potential of pine plantations compared to other natural vegetation types including second-growth forests and mature forests. Specifically, I tested several predictions relating patterns of number of bird species with forest types. I examined predictions concerning forest specialist and forest generalist species guilds. Forest specialists are bird species that are assumed intolerant to forest disturbances. Forest generalists are bird species that inhabit all forest types and are assumed to be more tolerant of forest disturbances. Natural forest has very complex vegetation composition and structure, and is hypothesized to support a larger number of bird species, especially forest specialist species, than plantation forests. Therefore, I predicted 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, second-forests and pine plantations. Addionally, I predicted that total species richness (number of bird species) will be highest in mature forest and lower in second-growth forest and pine plantations.

METHODS

Study area

The study area was in Tam Dao National Park (TDNP), Vietnam (21° 21' – 21° 42' N; 105° 23' – 105° 44' 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 maximum temperature of 41.5°C. The park receives ~16 cm precipitation annually and relative humidity averages 82%.

TDNP supports 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 second-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. Second-growth forest results from intense logging and wood gathering. Second-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 Horsetail Pine plantation (*Pinus massoniana*) that is an introduced species. The pine plantations were 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: mature forest, second-growth forest, and pine plantation. Sampling effort, both in terms of person-hours and area sampled, was approximately the same in all three forest types 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 of which are preferable to conventional 'observed number of species' (Walther and Morand 1998, Walther and Moore 2005). Considerable 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) can not be utilized. In addition, these estimators 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 been used much 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 that partitions individuals into finite groups (or mixtures) 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 to estimate number of bird species.

I estimated 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 within each vegetation type). An encounter history was constructed for each 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 index, singing propensity and body length (see Table 1.1 for definitions, values in Appendix II) were used as covariates to test predictions concerning detection probabilities. I thought the regional commonness index 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 (ΔAICc), AICc weight (w_i), and and cumulative AICc weights (Σw_i) (Burnham and Anderson 2002). Cumulative AICc weight for a given covariate is the sum of AICc weight of all models that contain that covariate. The main candidate models were: (1) equal detection probabilities (p) in the three vegetation types ($P_{MF=SG=PP}$), where MF = mature forest, SG = second-growth forest, and PP = pine plantation), (2) equal detection probabilities in mature forests and second-growth, with pine plantations being different ($P_{MF=SG\#PP}$); (3) equal detection

probabilities in second-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 vegetation types, I also modeled detection probabilities as a function of survey occasion (t) as an additive (+) and interactive (*) effect. With each of these models I also added covariate effects of observer, singing propensity, body length, and regional commonness index separately or in combination. A total of 128 models were constructed for each analysis estimating number of forest specialist species and number of forest generalist species. Parameters of interest were model-averaged across the entire model set. Overall species richness were then estimated by adding number of forest specialist and forest generalist species and variance of the estimate was calculated using Delta medthod (Powell 2007).

RESULTS

Raw data

Observers recorded 3648 individual birds and detected 71, 60, and 45 avian species in mature forest, second-growth forest, and pine plantations, respectively. These species belonged 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, with 46, 24, and 14 forest specialist species detected in mature forest, second-growth forest, and pine plantation, respectively and 25, 36, and 31 forest generalist species detected in mature forest, second-growth forest, and pine plantation, respectively.

Forest specialist species

Models for forest specialist species in which detection varied by vegetation type had strong explanatory ability, with effects of vegetation type included in all models with $w_i > 0.01$ (Table 1.2). Models that included the effect of vegetation type were always selected over models that did not include this effect. Detection probability for forest specialist species was highest in mature forest, lower in second-growth forest, and least in pine plantation (Fig. 1.1). Models with time-varying detection probability did not have much explanatory value (Table 1.2). All models containing time effects had ΔAICc > 5.00 and AICc weight (w_i) < 0.01. Detection probabilities in two mixtures were substantially different (Fig. 1.1) indicating that 31% of species (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 1.2 and Fig. 1.2). Singing propensity ($\Sigma w_i = 0.52$) and body length ($\Sigma w_i = 0.45$) had similar but weaker influence on detection probability (Fig. 1.2). 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. Body length only occasionally appeared in the top models.

Based on model averaged 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 second-growth forest, and 49.45 (95% CI = 1.84, 97.06) in pine plantations (Fig. 1.3). There was considerable uncertainty in these estimates.

Forest generalist species

Models in which detection varied by vegetation type had strong support; all top models with low ΔAICc values contained effects of vegetation type (Table 1.3). Models incorporating observer and/or vegetation type effects were always selected over models not incorporating these effects. Detection probability was highest in pine plantation, lower in second-growth forest, and lowest in mature forest (Fig. 1.4). Models with time-varying detection probability did not have much explanatory value. All models containing time effects had ΔAICc > 6.00 and AICc weight (w_i) < 0.02 (Table 1.3). Detection probabilities in two mixtures were substantially different (Fig. 1.5) indicating that 26% of species (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 included 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 1.3). Singing propensity consistently

appeared in the top models and was the second best explanatory covariate (Table 1.3 and Fig. 1.5). Body length had weaker influence on detection probabilities than regional commonness index and singing propensity, and was included 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 second-growth forest, and 56.57 (95% CI = 31.28, 81.85) in pine plantation (Fig. 1.3). There was considerable uncertainty in these estimates.

Total species richness

Using estimates of number of forest specialist and generalist species, I estimated species richness to be 191.36 (95% CI = 95.99, 287.35) in mature forest, 157.92 (95% CI = 87.42, 245.34) in second-growth forest, and 106.02 (95% CI = 52.11, 158.13) in the 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 modeled some of this heterogeneity, the mixture structure was also needed to model

heterogeneity not accounted for by the covariates. 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; 26-31% of species were categorized as having a high detection probability, while the rest had very low detection probability. Although some top models contained 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 both analyses). The probability of detecting a species often increases with increased abundance of individual species (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, the effect of singing propensity ($\Sigma w_i = 0.52$) is much lower than in the the other analyse ($\Sigma w_i = 1.00$), possibly due to observers who 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 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 vegetation type 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 second-growth forest and pine plantations making the species detection probabilities in mature habitat higher than in other vegetation types in the analysis of forest specialist species (Fig. 1.1). In contrast, forest generalist species may be more abundant in second-growth forests and pine plantations than in mature forests. Therefore, in the analysis of forest generalists, detection probabilities in second-growth forests and pine plantations were higher than in mature forests (Fig. 1.4). Although forest generalist species may be more abundant in second-growth forest than in pine plantation, detection in pine plantation was still slightly higher than in second-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 second-growth forest and least in pine plantation although 95% confidence intervals overlapped for estimates in mature forest compared to second-growth forest and second-growth forest compared to pine plantation. The number of forest generalist species seems to be similar between mature forest and second-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 second-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). Second-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 vegetation types just by chance alone. Other two species are open country species. No species detected is unique to the pine plantations.

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 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, preventing seeds from reaching soils and inhibiting the regrowth and development of shrubs and native trees. The absence of fructivorous avian species, in turn, inhibits seed dispersal in pine plantations. The pine plantation canopy is also more permeable to light, causing the microclimate in the pine plantation understory to be drier than those under mature forest and second-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. In turn, this may reduce the overall insectivorous species and ground-feeding insectivores in pine plantations.

The availability of cavities and snags in second-growth may be less than in mature forest because second-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 second-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 second-growth and two species were detected in pine plantation.

Management Implications

Based on species richness, avian conservation value is probably highest in mature and second-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 was 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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Table 1.1. Individual covariates used in modeling detection probabilities (MF=mature forest, SG=Second-growth forest, PP=Pine plantation, and ALL = all habitats combined).

Covariate	Description	Range	Mean ± SD
Body length (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 ± 10.85 MF: 21.40 ± 8.51 SG: 20.32 ± 10.78 PP: 24.37 ± 13.76
Regional commonness index	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 ± 1.50 MF: 3.25 ± 1.61 SG: 3.33 ± 1.54 PP: 3.33 ± 1.26
Singing propensity	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 ± 0.41 MF: 0.74 ± 0.44 SG: 0.83 ± 0.38 PP: 0.80 ± 0.40

Table 1.2. Model selection results for forest specialist species based on 128 models describing detection probabilities in three vegetation types (MF=mature forest, SG=Second-growth forest, and PP=Pine plantation) and two observers (ob). Two mixtures were used with a common probability of inclusion (π) in each mixture across habitat types. Detection probability was modeled as being similar in the three vegetation types ($P_{MF=SG=PP}$), as similar in the mature and second-growth forests only ($P_{MF\#SG=PP}$), as similar in the second-growth and pine plantations only ($P_{MF\#SG=PP}$), and as different for all vegetation types ($P_{MF\#SG\#PP}$). 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 vegetation types and other covariates, detection probabilities were also modeled as a function of survey occasion (t) as an additive (+) and interactive (*) effect. Models are ranked by AICc. ΔAICc is the difference in AICc units from the highest ranking model, w_i indicates AICc weights, L is the model likelihood, K is the number of model parameters, and D is deviance. 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 (-2log × likelihood) of the current model and (-2log × likelihood) of the saturated model.

Model	AICc	ΔAICc	w_i	L	K	D
$P_{(MF\#SG\#PP,\ co)}$	582.89	0.00	0.10	1.00	7	568.67
$P_{(MFF\#SG\#PP,\ co,\ si,\ bo)}$	583.37	0.48	0.08	0.79	9	565.01
$P_{(MFF\#SG\#PP,\ co,\ si)}$	583.66	0.77	0.07	0.68	8	567.37
$P_{(MFF\#SG=PP,\ co,\ si,\ bo)}$	583.73	0.83	0.06	0.66	8	567.43
$P_{(MF\#SGG=PP,\ co)}$	583.81	0.91	0.06	0.63	6	571.64
$P_{(MF\#SGG=PP,\ co,\ si)}$	583.90	1.01	0.06	0.60	7	569.68
$P_{(MF\#SG\#PPPP,\ ob,\ co,\ bo)}$	584.06	1.16	0.05	0.56	9	565.69
$P_{(MF\#SG\#PPPP,\ ob,\ co)}$	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
$P_{(MF\#SG\#PP,\ ob,\ co,\ si,\ bo)}$	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
$P_{(MF\#SG\#PP,\ ob,\ co,\ si)}$	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
$P_{(MF\#SG=PP,\ ob,\ co,\ si,\ bo)}$	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
$P_{(MF\#SG=PP,\ ob,\ co,\ si)}$	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
$P_{(MF=SG\#PP,\ co,\ si,\ bo)}$	585.58	2.69	0.03	0.26	8	569.29
$P_{(MF\#SG=PP,\ ob,\ co,\ bo)}$	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
$P_{(MF=SG\#PP,\ ob,\ co,\ si)}$	586.19	3.29	0.02	0.19	8	569.90
$P_{(MF=SG\#PP,\ ob,\ co,\ si,\ bo)}$	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

...table continued

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Model	AICc	ΔAICc	w_i	*L*	*K*	*D*
$P_{(MF\#SG\#PP,\ +t,\ co,\ si,\ bo)}$	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
$P_{(MF\#SG=PP,\ +t,\ co,\ si,\ bo)}$	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
$P_{(MF=SG=PP,\ ob,\ co,\ si)}$	593.79	10.90	0.00	0.00	7	579.56
$P_{(MF=SG=PP,\ ob,\ co,\ bo)}$	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
$P_{(MF=SG=PP,\ ob,\ co,\ si,\ bo)}$	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
$P_{(MF\#SG\#PP,\ co,\ bo)}$	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
$P_{(MF\#SG=PP)}$	600.68	17.79	0.00	0.00	4	592.60
$P_{(MF=SG\#PP)}$	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
$P_{(MF=SG=PP,\ ob,\ bo)}$	601.59	18.70	0.00	0.00	5	591.47
$P_{(MF=SG=PP,\ si)}$	601.78	18.88	0.00	0.00	4	593.70
$P_{(MF\#SG=PP,\ ob)}$	601.87	18.97	0.00	0.00	5	591.75

...table continued

...table continued

Model	AICc	ΔAICc	w_i	L	K	D
$P_{(MF=SG\#PP,\ ob)}$	601.96	19.07	0.00	0.00	5	591.84
$P_{(MF=SG\#PP,\ bo)}$	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
$P_{(MF\#SG\#PP)}$	602.60	19.70	0.00	0.00	5	592.47
$P_{(MF\#SG=PP,\ ob,\ bo)}$	602.81	19.91	0.00	0.00	6	590.64
$P_{(MF\#SG=PP,\ si)}$	602.95	20.05	0.00	0.00	5	592.83
$P_{(MF=SG=PP,\ ob,\ si)}$	602.98	20.08	0.00	0.00	5	592.85
$P_{(MF\#SG=PP,\ bo)}$	603.30	20.41	0.00	0.00	5	593.18
$P_{(MF=SG\#PP,\ ob,\ bo)}$	603.40	20.51	0.00	0.00	6	591.23
$P_{(MF\#SG\#PP,\ bo)}$	603.65	20.76	0.00	0.00	6	591.48
$P_{(MF=SG=PP,\ *t,\ co,\ si)}$	603.70	20.81	0.00	0.00	21	559.79
$P_{(MF\#SG\#PP,\ ob)}$	603.79	20.89	0.00	0.00	6	591.62
$P_{(MF=SG=PP,\ si,\ bo)}$	603.79	20.90	0.00	0.00	5	593.67
$P_{(MF=SG\#PP,\ si)}$	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
$P_{(MF\#SG=PP,\ ob,\ si)}$	604.15	21.26	0.00	0.00	6	591.98
$P_{(MF\#SG\#PP,\ si)}$	604.44	21.55	0.00	0.00	6	592.27
$P_{(MF=SG=PP,\ *t,\ co,\ si,\ bo)}$	604.84	21.95	0.00	0.00	22	558.74
$P_{(MF\#SG\#PP,\ ob,\ bo)}$	604.85	21.96	0.00	0.00	7	590.62
$P_{(MF\#SG=PP,\ si,\ bo)}$	604.91	22.01	0.00	0.00	6	592.74
$P_{(MF=SG=PP,\ ob,\ si,\ bo)}$	605.00	22.10	0.00	0.00	6	592.83
$P_{(MF=SG\#PP,\ ob,\ si)}$	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
$P_{(MF\#SG\#PP,\ ob,\ si)}$	605.65	22.76	0.00	0.00	7	591.43
$P_{(MF=SG\#PP,\ si,\ bo)}$	605.83	22.93	0.00	0.00	6	593.66
$P_{(MF\#SG=PP,\ ob,\ si,\ bo)}$	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
$P_{(MF=SG\#PP,\ ob,\ si,\ bo)}$	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
$P_{(MF\#SG\#PP,\ ob,\ si,\ bo)}$	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
$P_{(MF=SG=PP,\ +t,\ si,\ bo)}$	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

...table continued

...table continued

Model	AICc	ΔAICc	w_i	L	K	D
$P_{(MF\#SG=PP,\ +t,\ si,\ bo)}$	610.84	27.94	0.00	0.00	11	588.30
$P_{(MF\#SG=PP,\ *t,\ co,\ bo)}$	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
$P_{(MF\#SG\#PP,\ *t,\ co,\ si,\ bo)}$	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
$P_{(MF=SG=PP,\ *t,\ si,\ bo)}$	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
$P_{(MF=SG=PP,\ *t,\ si)}$	616.59	33.70	0.00	0.00	19	577.02
$P_{(MF\#SG=PP,\ *t,\ si)}$	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
$P_{(MF=SG\#PP,\ *t,\ si,\ bo)}$	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
$P_{(MF\#SG\#PP,\ *t,\ si)}$	618.61	35.71	0.00	0.00	21	574.69
$P_{(MF\#SG=PP,\ *t,\ si,\ bo)}$	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 1.3. Model selection results for forest generalist species based on 128 models describing detection probabilities in three vegetation types (MF=mature forest, SG=Second-growth forest, and PP=Pine plantation) and two observers (ob). Two mixtures were used with a common probability of inclusion (π) in each mixture across habitat types. Detection probability was modeled as being similar in the three vegetation types ($P_{MF=SG=PP}$), as similar in the mature and second-growth forests only ($P_{MF=SG\#PP}$), as similar in the second-growth and pine plantations only ($P_{MF\#SG=PP}$), and as different for all vegetation types ($P_{MF\#SG\#PP}$). 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 vegetation types and other covariates, detection probabilities were also modeled as a function of survey occasion (t) as an additive (+) and interactive (*) effect. Models are ranked by AICc. ΔAICc is the difference in AICc units from the highest ranking model, w_i indicates AICc weights, L is the model likelihood, K is the number of model parameters, and D is deviance. 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 (-2log × likelihood) of the current model and (-2log × likelihood) of the saturated model.

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

...table continued

...table continued

Model	AICc	ΔAICc	w_i	L	K	D
$P_{(MF=SG\#PP,\ ob,\ co)}$	624.68	16.42	0.00	0.00	7	610.48
$P_{(MF\#SG=PP,\ +t,\ co,\ si)}$	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
$P_{(MF=SG=PP,\ *t,\ co,\ si,\ bo)}$	626.39	18.13	0.00	0.00	22	580.48
$P_{(MF\#SG=PP,\ *t,\ co,\ si)}$	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
$P_{(MF=SG=PP,\ ob,\ co,\ si,\ bo)}$	627.08	18.82	0.00	0.00	8	610.82
$P_{(MF\#SG=PP,\ co,\ bo)}$	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
$P_{(MF\#SG\#PP,\ ob,\ si,\ bo)}$	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
$P_{(MF=SG=PP,\ co,\ si)}$	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
$P_{(MF=SG=PP,\ co,\ si,\ bo)}$	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
$P_{(MF=SG\#PP,\ ob,\ si,\ bo)}$	631.91	23.65	0.00	0.00	7	617.70
$P_{(MF\#SG=PP,\ ob,\ si,\ bo)}$	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
$P_{(MF\#SG\#PP,\ si,\ bo)}$	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
$P_{(MF=SG=PP,\ +t,\ co,\ si,\ bo)}$	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
$P_{(MF\#SG=PP,\ *t,\ co,\ bo)}$	635.01	26.74	0.00	0.00	22	589.09
$P_{(MF=SG\#PP,\ si,\ bo)}$	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
$P_{(MF\#SG=PP,\ si,\ bo)}$	635.61	27.35	0.00	0.00	6	623.46
$P_{(MF\#SG\#PP,\ +t,\ si,\ bo)}$	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

...table continued

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Model	AICc	ΔAICc	w_i	*L*	*K*	*D*
$P_{(MF\#SG\#PP,\ *t,\ co,\ bo)}$	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
$P_{(MF=SG\#PP,\ +t,\ si,\ bo)}$	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
$P_{(MF\#SG\#PP,\ ob)}$	639.89	31.62	0.00	0.00	6	627.73
$P_{(MF=SG\#PP)}$	639.95	31.69	0.00	0.00	4	631.88
$P_{(MF\#SG\#PP,\ *t,\ co)}$	640.52	32.26	0.00	0.00	22	594.61
$P_{(MF=SG\#PP,\ *t,\ co)}$	641.03	32.77	0.00	0.00	21	597.28
$P_{(MF\#SG\#PP,\ ob,\ bo)}$	641.58	33.31	0.00	0.00	7	627.37
$P_{(MF=SG\#PP,\ bo)}$	641.96	33.70	0.00	0.00	5	631.85
$P_{(MF\#SG=PP,\ ob,\ si)}$	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
$P_{(MF\#SG\#PP)}$	643.47	35.20	0.00	0.00	5	633.36
$P_{(MF\#SG=PP,\ *t,\ si,\ bo)}$	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
$P_{(MF\#SG=PP,\ ob,\ bo)}$	644.69	36.43	0.00	0.00	6	632.54
$P_{(MF\#SG\#PP,\ bo)}$	645.20	36.93	0.00	0.00	6	633.04
$P_{(MF\#SG=PP,\ si)}$	645.81	37.55	0.00	0.00	5	635.70
$P_{(MF=SG=PP,\ *t,\ si,\ bo)}$	645.88	37.62	0.00	0.00	20	604.30
$P_{(MF\#SG\#PP,\ *t,\ si,\ bo)}$	646.20	37.94	0.00	0.00	22	600.29
$P_{(MF=SG=PP,\ ob,\ bo)}$	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
$P_{(MF=SG\#PP,\ *t,\ si,\ bo)}$	647.61	39.34	0.00	0.00	21	603.86
$P_{(MF=SG=PP,\ ob,\ si,\ bo)}$	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
$P_{(MF=SG=PP,\ ob)}$	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
$P_{(MF=SG=PP,\ ob,\ si)}$	648.65	40.39	0.00	0.00	5	638.54
$P_{(MF\#SG=PP,\ +t,\ si)}$	649.06	40.80	0.00	0.00	10	628.66
$P_{(MF=SG=PP,\ bo)}$	649.91	41.65	0.00	0.00	4	641.84
$P_{(MF=SG\#PP,\ si)}$	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
$P_{(MF=SG=PP,\ si,\ bo)}$	651.05	42.79	0.00	0.00	5	640.94
$P_{(MF\#SG=PP,\ +t,\ bo)}$	651.38	43.12	0.00	0.00	10	630.98
$P_{(MF=SG=PP)}$	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

...table continued

...table continued

Model	AICc	ΔAICc	w_i	*L*	*K*	*D*
$P(_{MF=SG=PP,}$ *si)*	652.06	43.80	0.00	0.00	4	643.99
$P(_{MF\#SG=PP,}$ *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
$P(_{MF=SG\#PP,}$ *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
$P(_{MF\#SG=PP,}$ **t, si)*	659.49	51.23	0.00	0.00	20	617.91
$P(_{MF\#SG\#PP,}$ **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
$P(_{MF=SG=PP,}$ **t, si)*	663.18	54.92	0.00	0.00	19	623.75
$P(_{MF=SG\#PP,}$ **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
$P(_{MF\#SG=PP,}$ **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

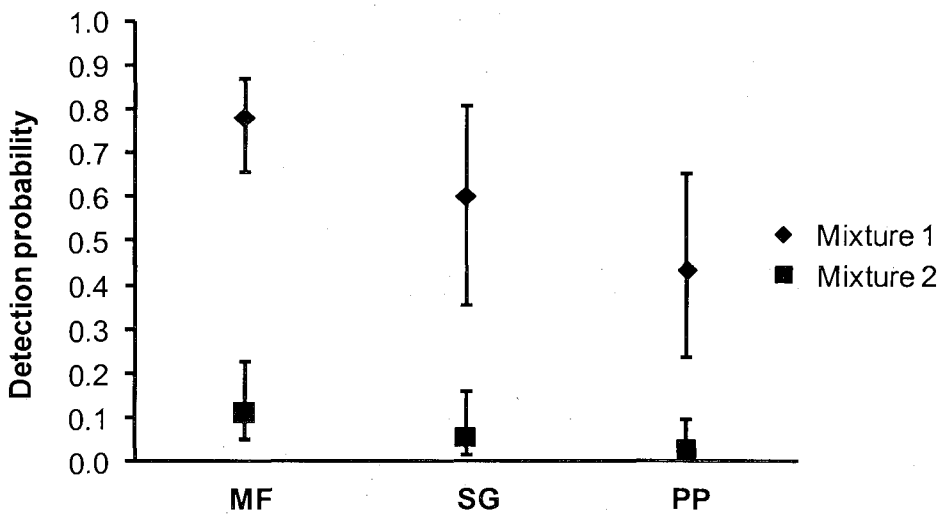

Figure 1.1. Model-averaged detection probability (with 95% confidence intervals) for the first occasion in the analysis of specialist species in different vegetation types (MF=mature forest, SG=second-growth forest, and PP=pine plantation). Species with high detection probabilities were categorized in mixture 1 and species with low detection probabilities are categorized in mixture 2.

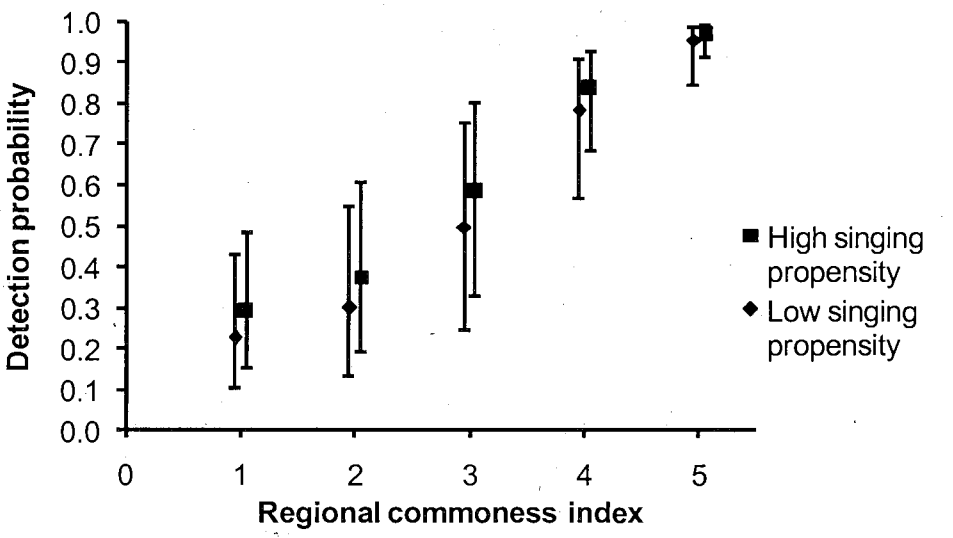

Figure 1.2. Model-averaged detection probability (with 95% confidence intervals) of species with high and low singing propensity during the first occasion for the higher detection probability mixture in mature forest for the forest specialist species.

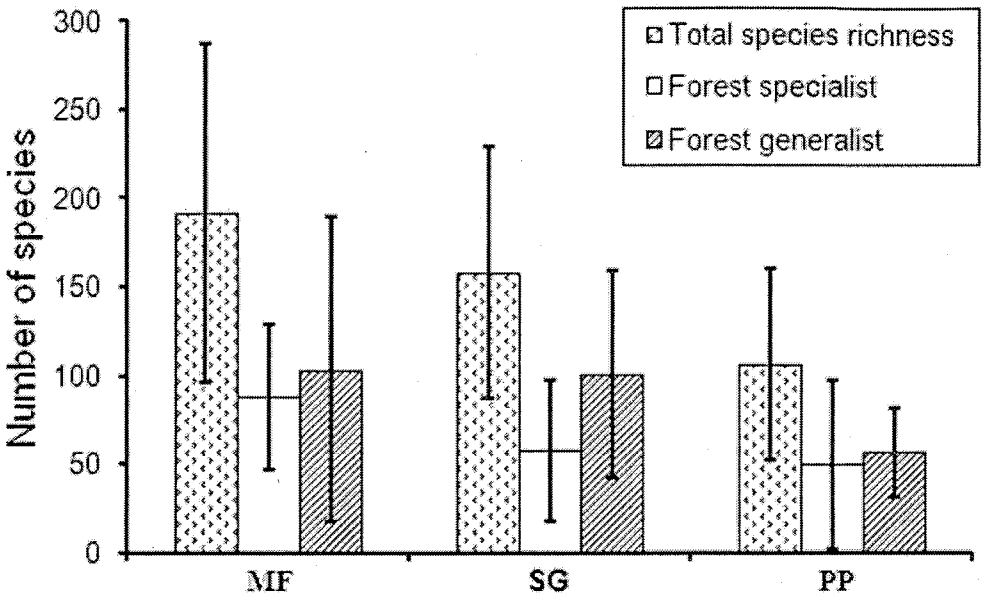

Figure 1.3. Model-averaged species richness estimates (with 95% confidence intervals) for different vegetation types (MF=mature forest, SG=second-growth forest, and PP=pine plantation).

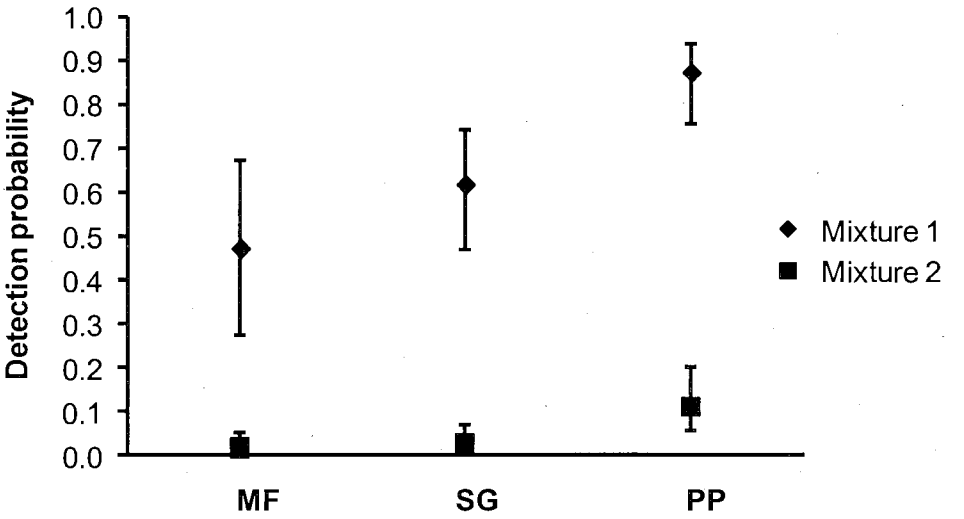

Figure 1.4. Model-averaged detection probability (with 95% confidence intervals) for the first occasion in the analysis of generalist species in different vegetation types (MF=mature forest, SG=second-growth forest, and PP=pine plantation). Species with high detection probabilities were categorized in mixture 1 and species with low detection probabilities are categorized in mixture 2.

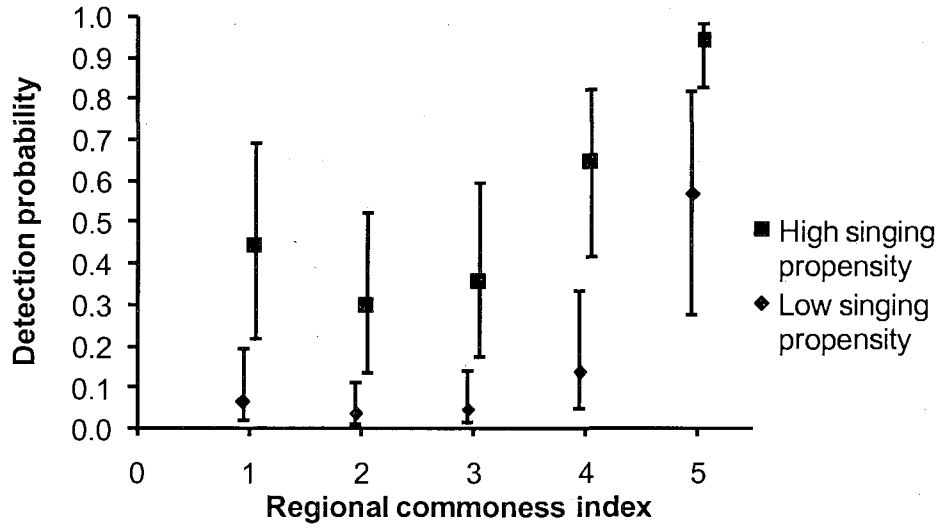

Figure 1.5. Model-averaged detection probability (with 95% confidence intervals) of species with high and low singing propensity during the first occasion for the higher detection probability mixture in mature forest for the forest generalist species.

CHAPTER 2

ROAD CROSSING BY BIRDS IN A TROPICAL FOREST IN NORTHERN VIETNAM

Abstract: Gaps, such as those caused by roads and powerlines, may 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. However, no such studies have been conducted in tropical Southeast Asia. Using playbacks of territorial calls, 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 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 longer 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 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 some wildlife species, 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 land development.

Using playbacks of territorial calls, I examined whether forest birds in Southeast Asia are inhibited from crossing roads by comparing 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° 14' – 20° 24' N; 105° 29' – 105° 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 was not disturbed and was 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 (T. T. 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 1.0 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 estimated a sample size of $n = 48$ for my "treatment" (road) and reference (forest interior) groups as sufficient to detect an effect size of 20% with a power of 80% and $\alpha = 0.05$ (Zar 1998).

Data Analysis

Data on presence and absence of responses 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.

For trials in which birds responded, data on the duration from the start of playback call to bird's approaching playback (response delay time) 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 corrected for small sample size (AICc) was used to rank models with the factors that influenced both species responses and their response delay time. Additionally, AICc weights (w_i) and cumulative AICc weights (Σw_i) were used to assess the strength of a given model and covariate in explaining the data (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 Σw_i) for the road factor. The adjusted cumulative AICc weight helped to reduce the bias in ranking the covariates resulted from differences in number of times covariates appearing in the

model set. 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 ($w_i = 0.27$, and ΔAICc = 0.62; Table 2.1). Models containing an interaction between road and species also had some support ($w_i = 0.16$, and ΔAICc = 1.68) as did a model containing an interaction between road and foraging height ($w_i = 0.11$, and ΔAICc = 2.36; Table 2.1). By examining the cumulative AICc weight (Σw_i), there was evidence that variation in the probability of approaching the playback was influenced by foraging height ($\Sigma w_i = 0.57$), road (adjusted $\Sigma w_i = 0.54$), and species ($\Sigma w_i = 0.43$; Table 2.1 and Fig. 2.1). Four top models with total

AICc weight of 0.9 may have similar biological meaning because of the dependence between foraging height and species; 2 species forage on the ground and 2 species forage in the canopy. The effect of road on the probability of approaching the playback varied by species and/or 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) and the odds of these birds crossing in the interior versus the road was 1.82 and 1.82, respectively (Table 2.2). Ground-foraging species (Puff-throated Babbler and Buff-breasted Babbler) were more prone to be affected by the road. Buff-breasted Babblers showed the greatest reduced probability of approaching the playback at the road (Fig. 2.1) and the odds of the ground-foraging species (Puff-throated Babbler and Buff-breasted Babbler) crossing the interior versus the road was 1.67 and 2.08, respectively as compared to the road (Table 2.2). 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 ΔAICc = 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 2.3). The second best model incorporated foraging height as the explanatory variable (w_i = 0.25, ΔAICc = 0.57) while models including the interaction between road and foraging height (w_i = 0.18, ΔAICc = 1.24) and road and species (w_i = 0.12, ΔAICc = 1.99) had some support. These results indicated that the response delay time was influenced mostly by foraging height (Σw_i = 0.76) and some by the effect of road (adjusted Σw_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 and 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. Anecdotally, their singing rate and volume of the response calls increased when individuals were in proximity of the playback. 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.

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 and, hence, reduced open area to be crossed.

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, especially for the mid-canopy species. 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 concern, 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. ΔAICc is the difference in AICc units from the highest ranking model. AICc weights (w_i), model likelihood (L), -2Loglikehood (-2Log$L$), 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	w_i	L	-2Log$L$	K	D
Logit(Prob) = Road + Species	334.21	0.00	0.36	1.00	324.07	5	4.53
Logit(Prob) = Road + Height	334.84	0.62	0.27	0.73	328.78	3	9.24
Logit(Prob) = Road + Species + Road*Species	335.89	1.68	0.16	0.43	319.54	8	0.00
Logit(Prob) = Road + Height + Road*Height	336.58	2.36	0.11	0.31	328.48	4	8.94
Logit(Prob) = Height	338.04	3.82	0.05	0.15	334.01	2	14.47
Logit(Prob) = Species	338.15	3.93	0.05	0.14	330.05	4	10.51
Logit(Prob) = Road	349.51	15.29	0.00	0.00	345.48	2	25.94
Logit(Prob) = intercept only	353.60	19.38	0.00	0.00	351.59	1	32.05

Table 2.2. Odds ratios of habitat (forest interior/road) in the probability of approaching the playback for different species.

Bird group	Odds ratio	Value
Mid-canopy foraging species	Striped Tit Babbler and forest interior /Striped Tit Babbler and road	1.82
	Rufous-throated Fulvetta and forest interior /Rufous-throated Fulvetta and road	1.82
Ground-feeding species	Puff-throated Babbler and forest interior/ Puff-throated Babbler and road	1.67
	Buff-breasted Babbler and forest interior/ Buff-breasted Babbler and road	2.08

Table 2.3. 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. ΔAICc is the difference in AICc units from the highest ranking model. AICc weights (w_i), model likelihood (L), -2Loglikehood (-2Log$L$), 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	w_i	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

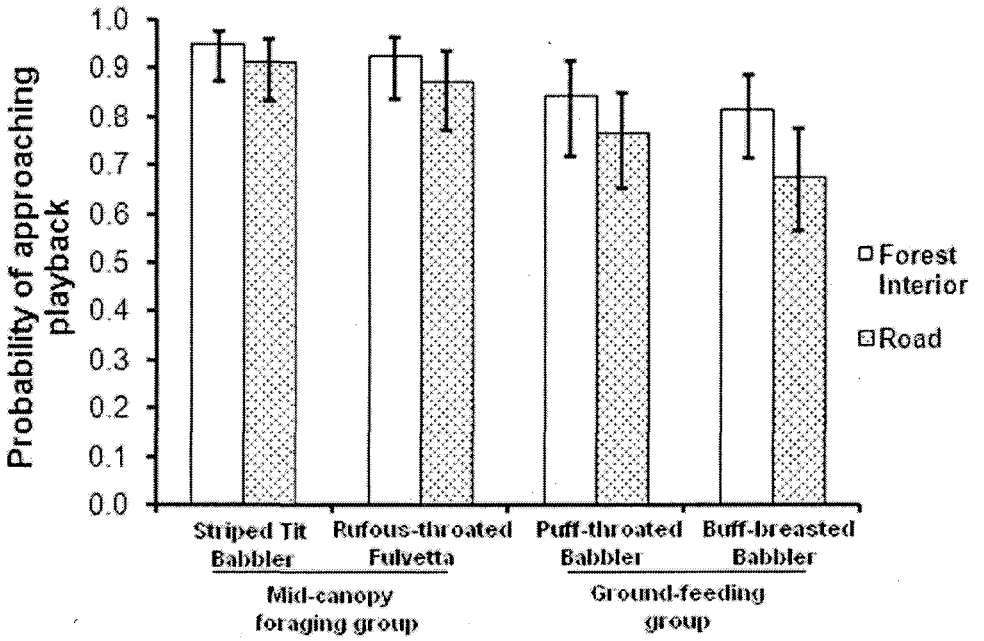

Figure 2.1. Model-averaged probability of approaching playback calls by species and habitat types (with 95% confidence intervals).

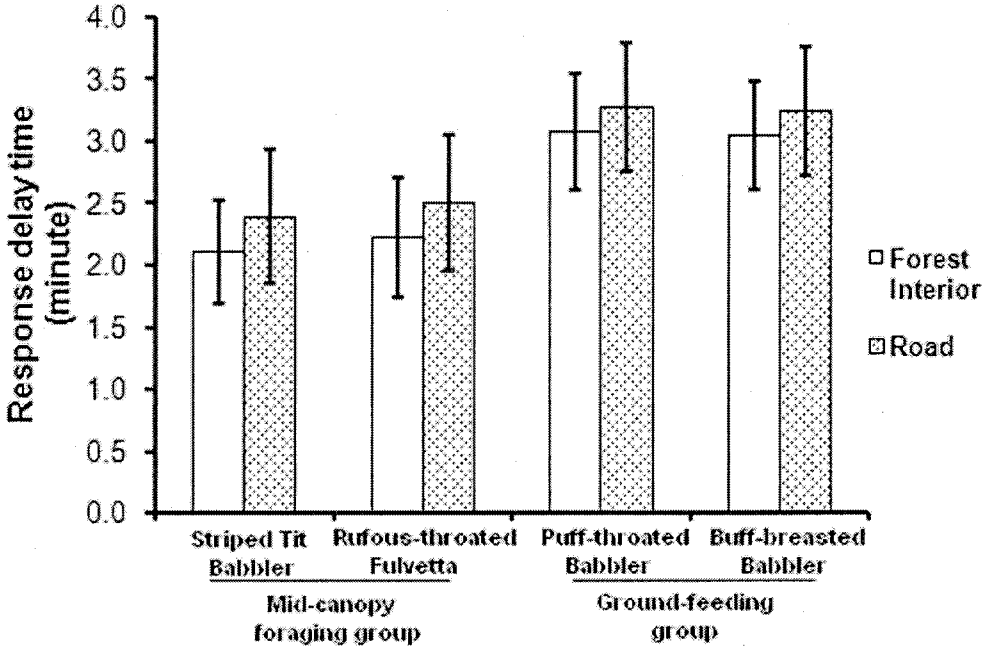

Figure 2.2. Model-averaged response delay time (minutes) by species and habitat types (with 95% confidence intervals).

CHAPTER 3

EFFECTS 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 throughout the tropics of Asia, leading to the local extinction of many bird populations. Much of the remaining forest is also being altered to disturbed or second growth forests. Most of the tropical forests in Asia are located in developing countries, which heavily utilize their natural resources, such as tropical forests, for development. Thus, setting aside remaining natural forests for conservation purposes is nearly 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 need to be more thoroughly understood. To address this, I simulated 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. Based on simulation models, the recovery processes of these two groups of species associated with the forest succession gradient was different and led to changes in avian communities. The recovery rate of forest generalists was very high

during the first 15 years of succession and then became asymptotic. The recovery rate of forest specialists remained high until about 50 years of succession. After 50 years, the recovery rate was lower, and fewer bird species colonized 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. The results from these simulations suggested that logging schemes with either cycle lengths > 40 years or wood volume left after harvest > 55% should be implemented to conserve 80% of the species pool. 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 than 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 throughout 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 converted 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) simulated 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, the results from Kohler et al. (2002) cannot be appropriately used for inference to tropical evergreen forest ecosystems; similar studies are needed to better understand how bird communities might recover from logging in the evergreen forests. In this chapter, I addressed this need by simulated the effects of logging in evergreen forest on bird communities in Vietnam.

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 was to better understand the recovery process for avian communities under differing logging schemes in tropical evergreen forests. My study simulated the effect of different logging schemes on avian biodiversity and I provided recommendations concerning logging cycle lengths and the amount of wood volume that should be left after logging events.

METHODS

Forest growth model and logging schemes

I simulated forest growth and succession using the forest growth and yield model MYRLIN (Alder et al. 2002) and data from 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. When needed, I therefore 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 (LC; 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 (WL, 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. 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 developed 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):

$$y_i = \frac{44.8187i}{6.1084 + i} \qquad (1)$$

where y_i 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:

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

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:

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

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_i and g_i. I then generated a random number between 0 and 1for each species and individually compared the number with p_i or g_i 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). I ran 1000 simulations for each logging scheme for a total of 441,000 simulations. 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).

In the simulation modeling process, I also assumed that (1) the forest growth model was valid, (2) detection probabilities among different habitats in the study by Raman (1998) were equal to one (or at least were similar among habitats), (3) individual bird species within the same category (forest specialist or forest generalist) have the same turnover rate for a given forest age, (4) the recovery of a species is independent of other species, and (5) the source for avian community recovery is sufficient.

RESULTS

In simulations where WL = 0 (i.e., clearcut logging) with 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% resulted in 70% of the forest generalist species pool being conserved. Logging schemes with either LC > 70 years or WL > 60% resulted in 80% of the forest generalist species pool being conserved (Fig. 3.2, Table 3.1). This is the maximum number of species that could be conserved within a forest stand at a particular age. Logging schemes with longer logging cycles and more wood left after harvesting did 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 affected forest specialist species (Fig. 3.1c). Logging schemes with either LC > 20 years or WL > 35% resulted 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 did not greatly affect the total species richness (Fig. 3.1e, f). In logging schemes with small amounts of wood left after harvesting, bird communities could recover if cutting rotation intervals are long enough (Fig. 3.1a, b, d). The most severe effect on the bird communities occurred if short logging cycles and high intensity wood harvesting plans are utilized (Fig. 3.1c). Logging schemes with either LC > 15 years or WF > 30% resulted 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 WL > 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 (see 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. 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, such secondary cavity nesters are not common in this system. The fifth assumption is that the source of species for community recovery is sufficient, which is probably met because birds are generally more mobile than other taxa and can colonize very distant sites. However, in designing logging schemes, I recommend that logged stands be close to late-succesional stands to ensure that the source of species for community recovery will be sufficient.

Based on my simulations, the recovery rate of forest generalists was very high during the first 15 years of succession and then becomes asymptotic (Fig. 3.1a, b). This may be due to the broad habitat requirements of forest generalists. My simulations, therefore, predict that 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 by 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) found that avian species richness will generally recover 20 years after clear cutting in tropical evergreen forest, which was 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 few bird species not represented in the forest stand, and 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).

My simulations predicted 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. In general, logging schemes with either LC > 40 years or WL > 55% should result in 80% of the overall forest bird species pool conserved in the region (Fig. 3.4, Table 3.3). The thresholds for these logging scheme can be met if sustainable forest production methods are followed, where sustainable forest harvesting is has a logging cycle > 60 years and wood volume left > 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. Incorporating economic data related to logging to determine optimal logging schemes to both optimize species richness and revenue would be a useful future avenue of research.

Finally, my simulation modeling efforts have been at the community level and have not focused on any specific species; 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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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).

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 3.2. 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	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 3.3. Percentage of the total forest bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).

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

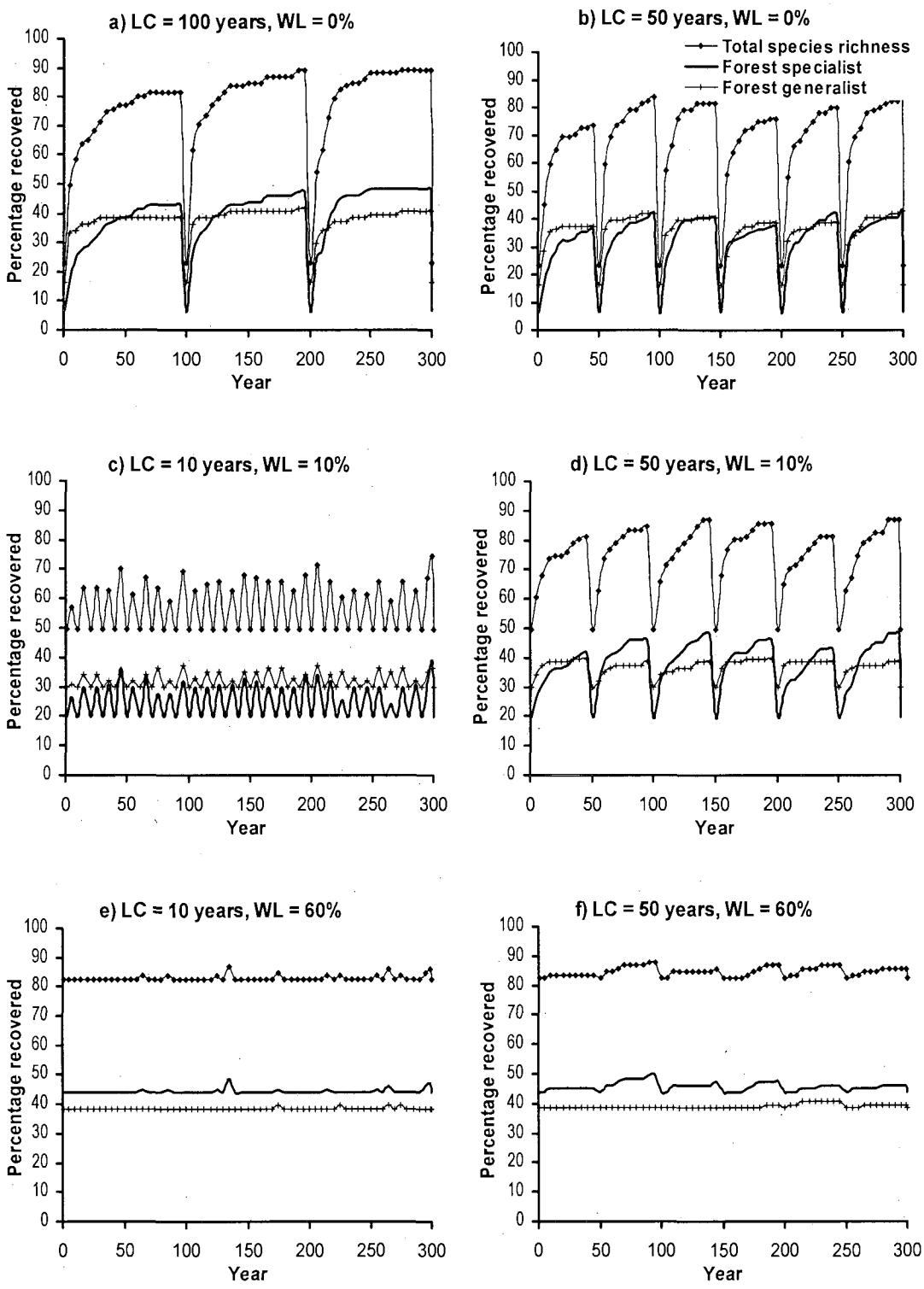

Figure 3.1a-f. Simulations of bird community dynamics along a succession gradient of a tropical evergreen forest under different logging schemes. LC = logging cycle, WL = wood volume left after harvesting.

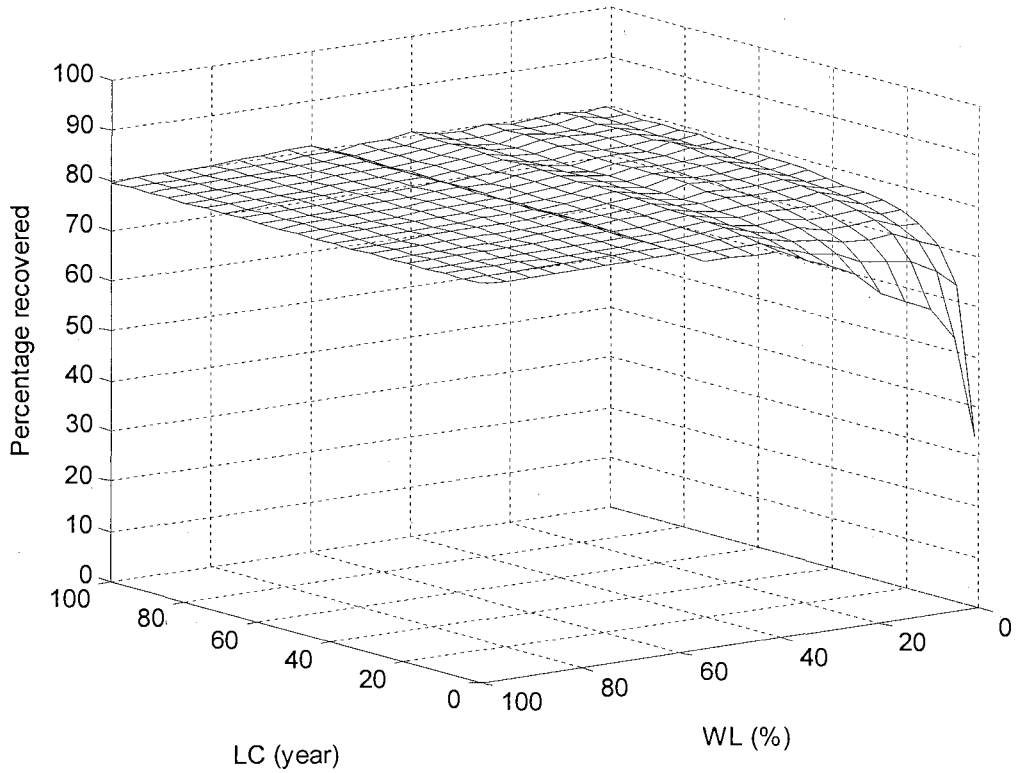

Figure 3.2. Percentage of the forest generalist bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).

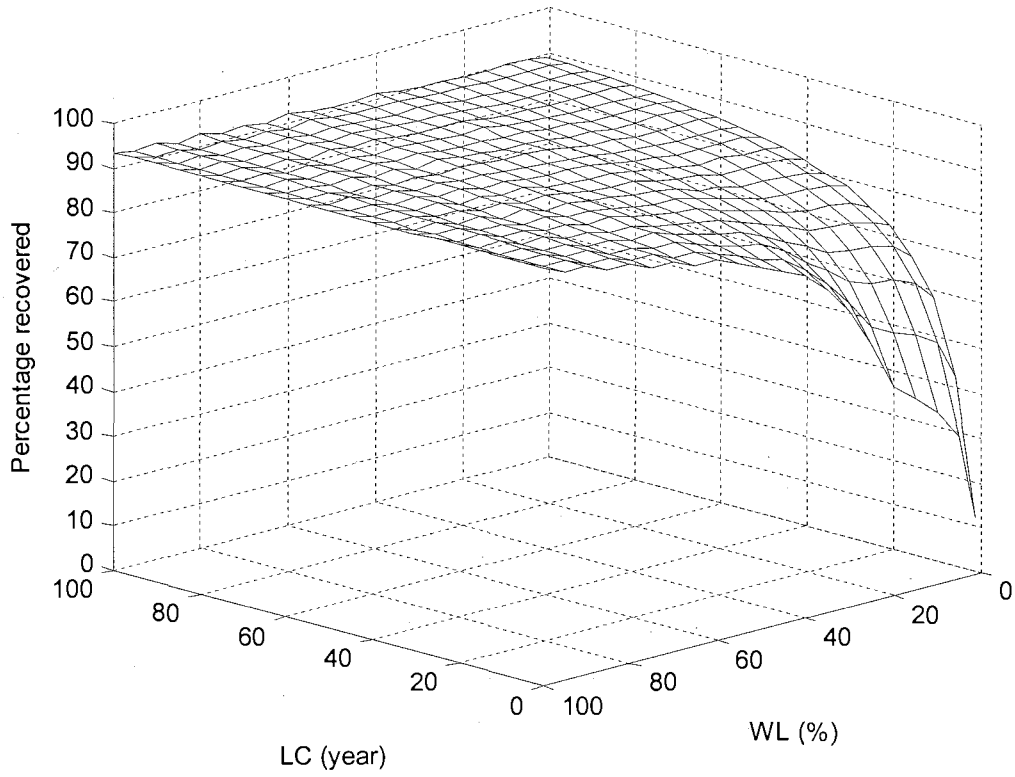

Figure 3.3. Percentage of the forest specialist bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).

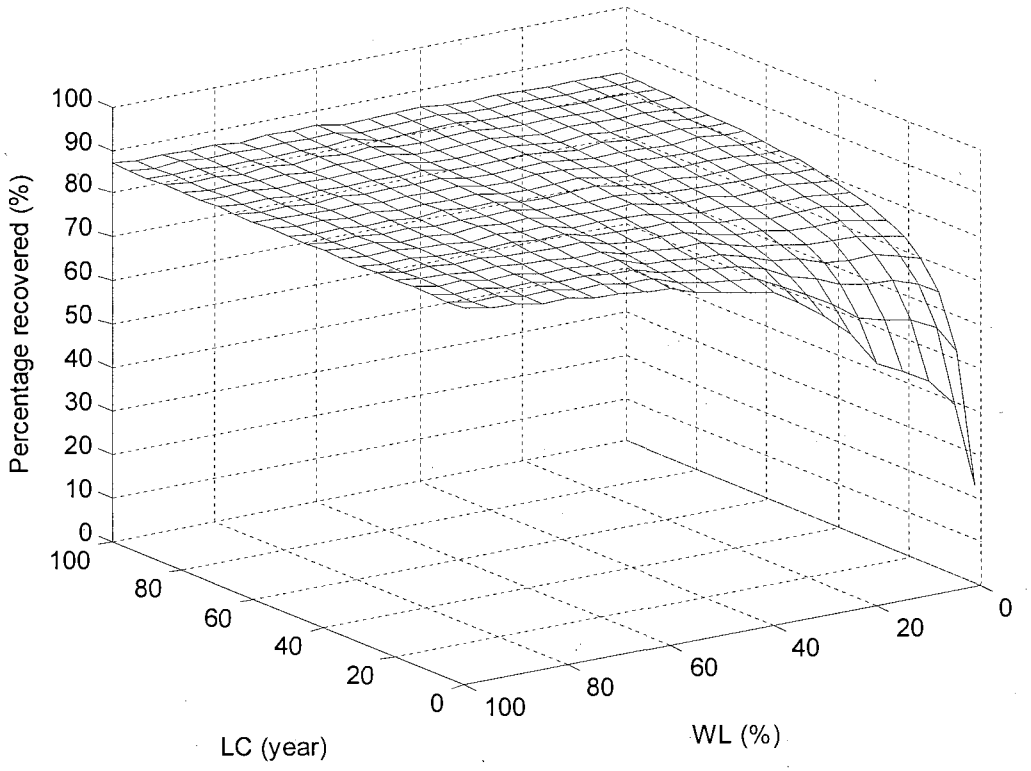

Figure 3.4. Mean percentage of the total forest bird species pool recovered as a function of logging cycle length (LC) and wood volume left after harvesting (WL).

CHAPTER 4

AVIAN MALARIA IN WILD BIRDS IN NORTHERN VIETNAM

Abstract: Wildlife diseases are gaining increasing attention given concerns about the role humans may play in emerging wildlife diseases and the impacts pathogens may have on vulnerable wildlife populations (Daszak et al. 2004). Avian blood parasites, or haemosporidia, make up one such group of parasites linked to critical conservation concerns. Given these concerns and a paucity of information on avian blood parasites in Vietnam, I characterized the prevalence of avian blood parasites that cause avian malaria and investigated the ecological factors affecting prevalence in free-ranging wild land birds. I focused on two genera of blood parasites, *Plasmodium* and *Haemoproteus* 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 also detected in the majority of bird species sampled. Prevalence of avian malaria parasites did not differ by sampling regions and habitats. However, higher parasite prevalence was observed in flocking than in solitary species and higher parasite prevalence was observed in adults than in juveniles. This is the first documented occurrence of AM in Vietnam.

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 (AM), have been implicated in the decline or loss of many naïve 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 such as mosquitoes (Culicidae). The effects of avian malarial parasites on hosts are very diverse. Disease symptoms of AM 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 rich in biodiversity and endemism (Nhat 2001).

Human encroachment and land use changes have been implicated in the emergence of many emerging diseases that contribute to the decline 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) that might be favorable for vector populations. 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 prevalence of infections with AM parasites (*Plasmodium spp.* or *Haemoproteus spp.*) in free-ranging wild land birds in northern Vietnam, and (2)

examining factors affecting the 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 predicted 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 were also examined. I predicted that flocking birds will have higher parasite prevalence than solitary birds because sociality is believed to enhance the transmission of disease pathogens among animals (Côté and Poulin 1995, Dobson 1988, Freeland 1976). Adult birds have a longer time of exposure to the vectors transmitting parasites (Ricklefs et al. 2005) relative to juveniles so I predicted that the prevalence will be higher in adult birds. Lastly, potential differences in prevalence in the two sampling region was investigated.

METHODS

Study sites

The research was conducted in Cuc Phuong National Park (CPNP; 20° 14' – 20° 24' N; 105° 29' – 105° 44' E; Appendix I) and Tam Dao National Park (TDNP; 21° 21' – 21° 42' N; 105° 23' – 105° 44' E; Appendix I) in northern Vietnam. The study area within TDNP is comprised of regrown forests that had been clearcut in the past while CPNP has not experienced similar 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 in each habitat 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 that initially had no or very low quality DNA detected.

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 μL of extracted DNA in 25μL volumes following procedures outlined in Beadell and Fleischer (2005). The final concentrations of components for these reactions were as follows: 0.6μM each primer, 1X PCR Gold buffer (Applied Biosystems), 2.0mM $MgCl_2$, 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 1.5μL of extracted DNA using illustra^{TM} puReTaq Ready-To-Go beads (GE Healthcare, Piscataway, NJ) with final primer concentrations of 0.5 μM of each primer. Several negative controls (i.e., distilled water) 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, Ipswich, Massachusetts) 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 presence and absence of parasites in individuals were analyzed using Proc LOGISTIC (SAS v.9.00, SAS 2002). I constructed 32 models with four main effect models that included: (1) prevalence (Prev) equal among the three habitat types $Ha_{(FI=FE=HL)}$, (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, $Ha_{(FI=FE\#HL)}$; (3) equal prevalence in forest edge and human-

dominated landscape, with forest interior being different, $Ha_{(FI\#FE=HL)}$; and (4) different prevalence for each of the three habitat types, $Ha_{(FI\#FE\#HL)}$. 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 observations. Prevalence was also modeled as constant over sampling region (Sr) (CPNP vs TDNP) and varying by sampling region. Akaike's Information Criteria corrected for small sample size (AICc) was used to rank models with the factors that influence avian malarial parasite prevalence. Additionally, AICc weights (w_i) and cumulative AICc weights (Σw_i) (see Chapter 1) were used to assess the strength of a given model and covariate in explaining the data (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 were screened for 256 birds from CPNP and 154 birds from TDNP (Appendix III). These birds represented 61 species and 15 families. Prevalence for avian malarial parasites was 45.31% (n = 116 positive birds) for birds caught in CPNP and 46.75% (n = 72 positive birds) for birds caught in TDNP. The overall prevalence for 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 blood parasite prevalence adequately (Table 4.1). A model in which prevalence was influenced by an additive combination between flocking behavior and age had the strongest support with $w_i = 0.27$. Flocking behavior and age also consistently appeared in the top models. Additionally, by examining the cumulative AICc weights, there was strong evidence that variation in prevalence was influenced by flocking behavior ($\Sigma w_i = 0.79$) and age ($\Sigma w_i = 0.94$). Flocking birds had higher prevalences than solitary bird species (Fig. 4.1) and the odds of the flocking birds carrying AM versus the solitary birds for adult and juvenile birds collected in the forest interior of Cuc Phuong National Park were 1.45 and 1.46, respectively (Table 4.2). Adult birds also had a higher prevalence than did juvenile birds (Fig. 4.1) and the odds of the adult birds carrying AM versus the juvenile birds for flocking bird and solitary birds collected in the forest interior of Cuc Phuong National Park were 2.12 and 2.14, respectively (Table 4.2).

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 low cumulative AICc weight ($\Sigma w_i = 0.27$). Accordingly, the overall estimate of prevalence for birds captured at Cuc Phuong National Park (45.31%) was similar to that of Tam Dao National Park (46.75%).

DISCUSSION

The overall avian malaria prevalence of 45.85% was considerably higher than a similar study conducted in Asia (including India, Myanmar, and South Korea) in which

the authors reported a 34.0% prevalence (Ishtiaq et al. 2007). This difference in prevalence might be attributed to differences in the climate or the species pool sampled between my study sites and theirs. Similarly high prevelances of AM in another study conducted in Japan were reported by 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, Ishtiaq et al. 2007, Ribeiro et al. 2005).

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 habitats 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. 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 (Côté and Poulin 1995, Dobson 1988, Freeland 1976). The higher prevalence among flocking birds in my study supports this hypothesis (Fig. 4.1). Flocks of Red-whiskered Bulbul, Black-crested Bulbul, Light-vented Bulbul, Striped Tit Babbler, Scaly-breasted 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). According to the encounter-dilution effect hypothesis, 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. Transmission of pathogens using vectors or intermediate hosts might be expected to correlate less with social group size than that of directly-transmitted pathogens (Moore et al. 1988). In the case of pathogens with vectors or intermediate hosts, there exists a lag time in transmission from one individual to another in the group. During that interval, the group size may change, and this weakens the negative relationship between group size and pathogen transmission. Additionally, the encounter-dilution effect might work for such cases in which the density of vectors is low. Because vectors are very abundant in the tropics, per capita number of bites 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 are solitary birds due to increased movement and increased CO_2 volume produced. 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 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, a 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 infected 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 initial 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 not express them in peripheral blood for detection (Atkinson and Van Riper III 1991, Ricklefs et al. 2005). This is particularly

the case for *Haemoproteus spp.* that require asexual schizogony in non-circulating blood cells before being expressed as gametocytes in peripheral blood.

In conclusion, the prevalence of AM infection in the birds I sampled was relatively high, infections were detected in the majority of species sampled, higher parasite prevalence was observed in flocking than solitary species, and higher parasite prevalence was observed in adult than in juvenile birds. Given the high prevalence, the broad host distribution of AM, and the paucity of information on the ecology of AM, I recommend additional studies to look at how parasite prevalence varies across seasons and to strengthen the dataset for additional 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 costs 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 alone was used to identify AM infections in birds. This technique underestimates true prevalence because infections from birds with low parasitemias tend to be very difficult to detect (Ribeiro et al. 2005); parasite infections 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 likely 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 to incomplete detection could be resolved by using estimators that account for the probability of detection, such as those used in capture-recapture estimators. This problem might also be alleviated by applying multiple primer sets to the samples.

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 nor investigate did I assess where parasite lineages from birds in Vietnam fit in the larger phylogeny of avian malarial parasites. This is the first study of AM parasites in birds inVietnam and my results suggest that an extraordinarily high number of bird species harbor blood parasites that cause AM. 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 at host species that were not 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 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) equal prevalence among the three habitat types, $Ha_{(FI=FE=HL)}$; (2) equal prevalence in forest interior and forest edge, with human-dominated landscape being different, $Ha_{(FI=FE\#HL)}$; (3) equal prevalence in forest edge and human-dominated landscape, with forest interior being different, $Ha_{(FI\#FE=HL)}$; and (4) different prevalence for each of the three habitat types, $Ha_{(FI\#FE\#HL)}$. Covariate effects of flocking behavior (Fb), age (Ag) and sampling region (Sr) were also used to model the prevalence separately or in combination. Models are ranked by AICc. ΔAICc is the difference in AICc units from the highest ranking model. AICc weights (w_i), model likelihood (L), -2Loglikehood (-2Log$L$), 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	w_i	L	-2LogL	K	D
Logit(Prev) = Fb + Ag	557.72	0.00	0.27	1.00	551.66	3	0.60
Logit(Prev) = $Ha_{(FI\#FE=HL)}$ + Fb + Ag	559.21	1.49	0.13	0.47	551.11	4	0.05
Logit(Prev) = $Ha_{(FI=FE\#HL)}$ + Fb + Ag	559.70	1.99	0.10	0.37	551.61	4	0.55
Logit(Prev) = Sr + Fb + Ag	559.74	2.02	0.10	0.36	551.64	4	0.59
Logit(Prev) = Ag	560.71	2.99	0.06	0.22	556.68	2	5.62
Logit(Prev) = $Ha_{(FI\#FE\#HL)}$ + Fb + Ag	561.21	3.50	0.05	0.17	551.07	5	0.01
Logit(Prev) = $Ha_{(FI\#FE=HL)}$ + Sr + Fb + Ag	561.26	3.54	0.05	0.17	551.11	5	0.05
Logit(Prev) = $Ha_{(FI\#FE=HL)}$ + Ag	561.47	3.76	0.04	0.15	555.41	3	4.36
Logit(Prev) = $Ha_{(FI=FE\#HL)}$ + Sr + Fb + Ag	561.75	4.03	0.04	0.13	551.60	5	0.55
Logit(Prev) = Sr + Ag	562.27	4.55	0.03	0.10	556.21	3	5.15
Logit(Prev) = $Ha_{(FI=FE\#HL)}$ + Ag	562.41	4.69	0.03	0.10	556.35	3	5.30
Logit(Prev) = Fb	563.12	5.40	0.02	0.07	559.09	2	8.04
Logit(Prev) = $Ha_{(FI\#FE=HL)}$ + Sr + Ag	563.24	5.53	0.02	0.06	555.15	4	4.09
Logit(Prev) = $Ha_{(FI\#FE\#HL)}$ + Sr + Fb + Ag	563.26	5.55	0.02	0.06	551.06	6	0.00
Logit(Prev) = $Ha_{(FI\#FE\#HL)}$ + Ag	563.51	5.79	0.01	0.06	555.41	4	4.35
Logit(Prev) = $Ha_{(FI=FE\#HL)}$ + Sr + Ag	564.17	6.45	0.01	0.04	556.07	4	5.02
Logit(Prev) = $Ha_{(FI\#FE=HL)}$ + Fb	564.68	6.96	0.01	0.03	558.62	3	7.57
Logit(Prev) = $Ha_{(FI=FE\#HL)}$ + Fb	564.71	6.99	0.01	0.03	558.65	3	7.59
Logit(Prev) = Sr + Fb	565.03	7.31	0.01	0.03	558.97	3	7.92
Logit(Prev) = $Ha_{(FI\#FE\#HL)}$ + Sr + Ag	565.24	7.53	0.01	0.02	555.10	5	4.04
Logit(Prev) = $Ha_{(FI=FE\#HL)}$ + Sr + Fb	566.45	8.74	0.00	0.01	558.36	4	7.30
Logit(Prev) = $Ha_{(FI\#FE=HL)}$ + Sr + Fb	566.53	8.81	0.00	0.01	558.43	4	7.38

...table continued

...table continued

Model	AICc	ΔAICc	w_i	L	-2LogL	K	D
Logit(Prev) = $Ha_{(FI \# FE \# HL)}$ + Fb	566.59	8.87	0.00	0.01	558.49	4	7.44
Logit(Prev) = Intercept only	567.57	9.85	0.00	0.01	565.56	1	14.50
Logit(Prev) = $Ha_{(FI \# FE = HL)}$	568.31	10.59	0.00	0.01	564.28	2	13.23
Logit(Prev) = $Ha_{(FI \# FE \# HL)}$ + Sr + Fb	568.35	10.64	0.00	0.00	558.21	5	7.15
Logit(Prev) = $Ha_{(FI = FE \# HL)}$	568.40	10.69	0.00	0.00	564.38	2	13.32
Logit(Prev) = Sr	569.51	11.79	0.00	0.00	565.48	2	14.42
Logit(Prev) = $Ha_{(FI \# FE \# HL)}$	570.02	12.30	0.00	0.00	563.96	3	12.90
Logit(Prev) = $Ha_{(FI \# FE = HL)}$ + Sr	570.33	12.61	0.00	0.00	564.27	3	13.22
Logit(Prev) = $Ha_{(FI = FE \# HL)}$ + Sr	570.43	12.72	0.00	0.00	564.37	3	13.32
Logit(Prev) = $Ha_{(FI \# FE \# HL)}$ + Sr	572.06	14.34	0.00	0.00	563.96	4	12.90

Table 4.2. Odds ratios for the prevalance of avian malaria for different bird groups collected in the forest interior of Cuc Phuong National Park in Summer 2007. The pattern of prevalence in birds collected in other habitat types in Cuc Phuong and Tam Dao National Parks is similar.

Odds ratio	**Value**
Adult and flocking/Adult and solitary	1.45
Juvenile and flocking/Juvenile and solitary	1.46
Flocking and adult/flocking and juvenile	2.12
Solitary and adult/Solitary and juvenile	2.14

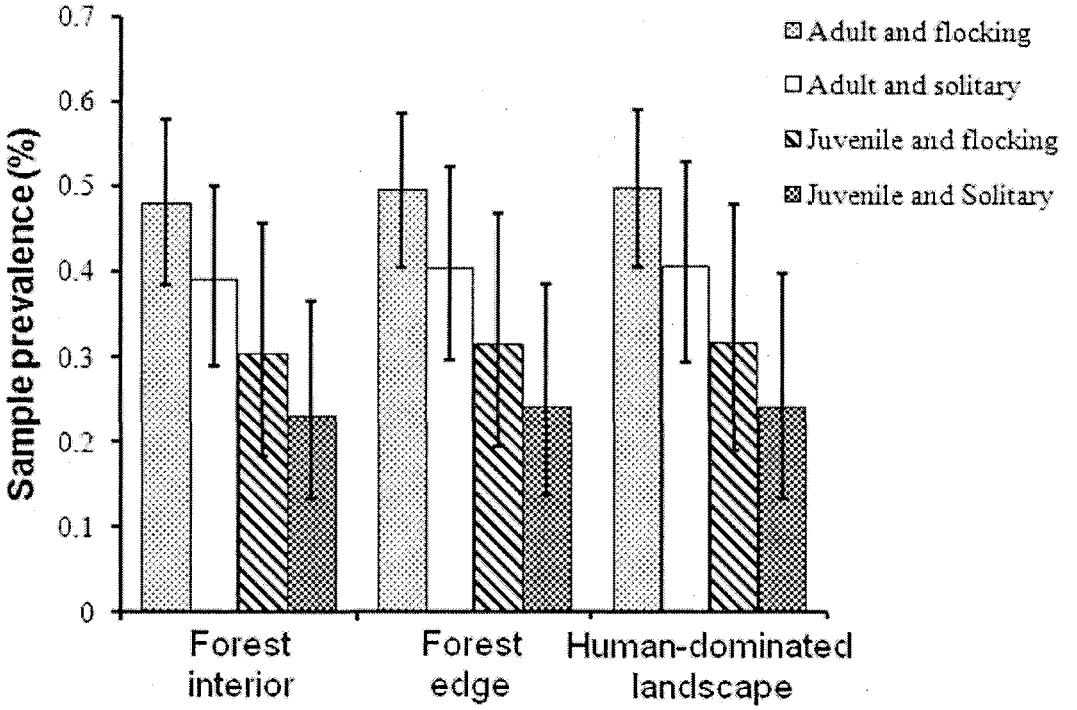

Figure 4.1. Avian malaria prevalence in birds collected in Cuc Phuong National Park in Summer 2007 (with 95% confidence intervals). The pattern of prevalence in birds collected in Tam Dao National Park is similar.

CHAPTER 5

AVIAN INFLUENZA VIRUS IN WILD LAND BIRDS IN NORTHERN VIETNAM

Abstract: Avian influenza viruses (AIVs) are currently considered one of the most important bird-associated groups of zoonotic pathogens. However, little information is available about the occurrence of AIVs in land birds, especially in Southeast Asia including Vietnam, an area that is experiencing a relatively high incidence of outbreaks of highly-pathogenic Asian-strain H5N1 in humans and domestic poultry. To begin to fill this information gap, my study focused on surveillance for the presence of AIV nucleic acids and antibodies for AIVs 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 an additional 193 birds and tested using rRT-PCR assay and virus isolation independently. Using an rRT-PCR assay alone, 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 two Puff-throated Bulbuls

(*Alophoixus pallidus*) tested positive with the rRT-PCR assay. 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 AIV RNA and two were positive for viable AIV, producing a prevalence of 7.25%. Tracheal swab samples made up 92.86% of positive sample and cloacal swab samples made up only 7.14% of positive samples, using both rRT-PCR and virus isolation. 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 AIV surveillance and monitoring programs. Among land birds, special attention should be given to the social, flocking species due to the higher AIV prevalence observed in this group compared to other groups. In particular, Japanese White-eyes may be an effective focal species in AIV 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, especially HPAI H5N1 in domestic poultry and the presence of HPAI viruses in land birds close to 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 viruses (AIVs) are currently considered one of the most important bird-associated groups of zoonotic pathogens. This is in large part due to 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 subtyped 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, AIVs 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 AIV-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 AIVs globally (e.g.,Gaidet et al. 2007, Iverson et al. 2008, Lei et al. 2007). While AIVs 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 viruses. However, emerging evidence indicates that land birds could play an important role in maintaining 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 AIVs 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 AIV nucleic acids and antibodies for AIVs in

free-ranging wild land birds in northern Vietnam. My study also sets the stage to investigate potential biological and ecological factors that could maintain the presence of AIVs in forest ecosystems.

METHODS

Study areas

The research was conducted in and near Cuc Phuong National Park (CPNP; 20° 14' – 20° 24' N; 105° 29' – 105° 44' E; Appendix I) and Tam Dao National Park (TDNP; 21° 21' – 21° 42' N; 105° 23' – 105° 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 (T. T.Vu, pers. obs.). These domestic fowl can be infected from, or can infect, migratory birds with AIVs which also persist in water and aquatic environments for weeks and even months (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 AIVs 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. Samples were not processed to determine other hemagglutinin

subtypes or neuraminidase subtypes because of an inadequate amount of serum collected from small birds.

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 separately for two different targets: a) to detect the presence of AIV nucleic acids (RNA) and b) to detect viable virus by virus isolation (Fig. 5.1).

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 AIV RNA. I considered Ct values < 40 as 'positive'.

Separate 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). Based on both methods combined, 12 samples were positive for AIV RNA and two were positive for viable AIVs, producing a prevalence of 7.25%. Of these, tracheal swab samples were 92.86% (13 of 14) of the positive samples and cloacal swab samples were only 7.14% (1 of 14) of positive samples.

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 within CPNP 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 may produce antibodies against HPAI viruses and subsequently survive the infection. Given the fact that HPAI H5N1 is currently causing many outbreaks in Vietnam, the detection of antibodies against the H5 subtype in my study strengthens this hypothesis. By surviving the infection, land birds can play a role as a reservoir and circulate the AIVs 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, prevalence for the presence of AIVs was 7.25% using a combination of 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 Southeastern 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 prevalence could be an underestimate. My study results,

together with some recent studies that found a surprisingly high prevalence of AIVs in land birds (Gronesova et al. 2008, Kou et al. 2005), support the idea that land birds can be effective reservoirs of AIVs.

Sociality is believed to enhance the transmission of disease pathogens among animals (Côté and Poulin 1995, Dobson 1988, Freeland 1976) in part because pathogen transmission is usually density-dependent (Anderson and May 1979, Mccallum et al. 2001). Four out of five of the birds captured at CPNP, which were positive for AIV antibodies, 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 prevalence. If this species is considered alone, AIV prevalence is 14.93%. Given relatively high prevalences and that they are abundant and easy to capture, the Japanese White-eye could be a useful focal species for AIV 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 AIV 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 AIVs 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, the type of habitat does not seem to be tightly linked with the presence of AIVs 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 AIVs between land birds and migratory water birds might happen, instead, during the winter. Virus in land birds surviving AIV infection in the winter can then be eliminated or diminished to undetectable levels. Similarly, after eliminating the virus, antibodies might diminish to undetectable levels. These factors might account for the similarity between prevalence of AIVs in different habitat types recorded in this study in the summer. Understanding how AIVs are distributed among habitats and how migratory water birds and domestic poultry affect the prevalence of AIVs 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 AIVs, 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 of HPAI H5N1. In wild 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 AIVs detected to specific subtypes; however, a study that is geographically close to my study reported that 2.3% of sampled birds carried AIVs other than H5 subtypes (Peterson et al. 2008) suggesting that some of the infected birds in my study may actually carry LPAI viruses. 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 AIVs in land birds, I suggest collecting and processing both types of samples including tracheal (or oropharyngeal) and cloacal swabs for AIV detection.

In conclusion, more attention should be given to land birds in AIV surveillance and monitoring programs due to the role land birds may play in the circulation of AIVs and the paucity of AIV surveillance data on them. Among land birds, special attention should be given to the social, flocking species. In particular, Japanese White-eyes may be an effective focal species in AIV surveillance or monitoring programs in Southeast Asia. Experimental infection of Japanese White-eyes with HPAI would also be recommended to investigate how HPAI affects this species and how AIV is shed to

environment, hence, be transmitted to domestic poultry. 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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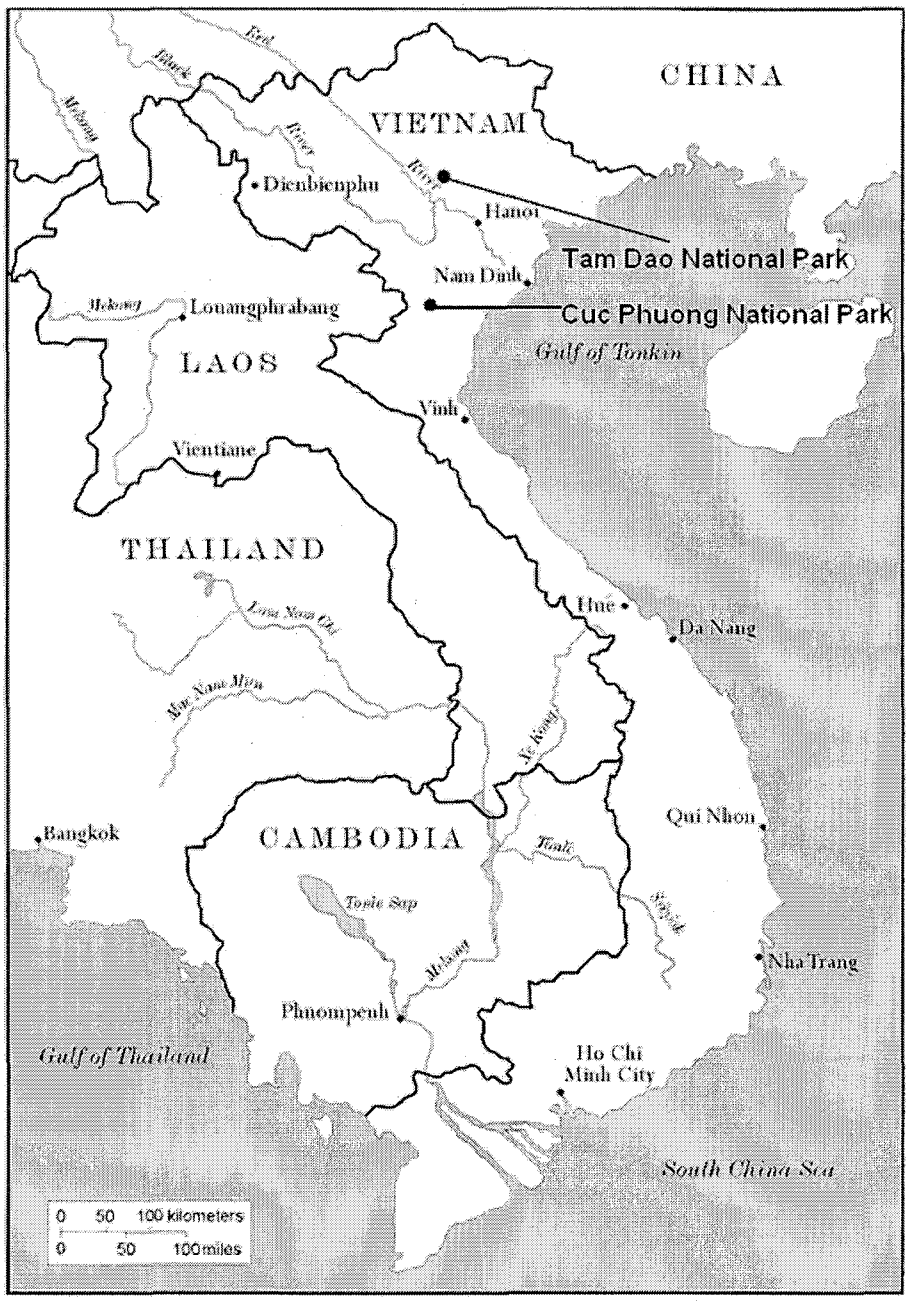
APPENDIX I

Locations of study areas



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=Second-growth forest, PP=Pine plantation, bo=body length (cm), co=regional commonness index[1], and si=singing propensity[2]).

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

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

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

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

[1.] 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.
[2.] 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.

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.

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

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English name	Scientific name	Number of birds	Number of infected birds
Red-flanked Bluetail	*Tarsiger cyanurus*	7	3
Oriental Magpie-Robin	*Copsychus saularis*	7	6
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
Nectariniidae	**Nectariniidae**		
Fork-tailed Sunbird	*Aethopyga christinae*	1	1
Crimson Sunbird	*Aethopyga siparaja*	1	1
Olive-backed Sunbird	*Arachnothera jugularis*	2	1

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English name	Scientific name	Number of birds	Number of infected birds
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

APPENDIX IV

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

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 paradise*	2
Large Woodshrike	*Tephrodornis gularis*	6
Muscicapidae	**Muscicapidae**	
Hainan Blue-Flycatcher	*Cyornis hainanus*	1
Snowy-browed Flycatcher	*Ficedula hyperythra*	1

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English name	Scientific name	Number of birds
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
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

APPENDIX V

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

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

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English name	Latin name	Cloacal swabs	Tracheal swabs
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