

FOREST PATCH OCCUPANCY BY SUMATRAN HORNBILLS IN A FRAGMENTED
LANDSCAPE OF SOUTHERN SUMATRA, INDONESIA

by

YOK YOK HADIPRAKARSA

(Under the Direction of JOHN P. CARROLL AND ROBERT J. COOPER)

ABSTRACT

Understanding habitat requirements for Sumatran hornbills at broad-scales are required for future conservation and management. I identified habitat relationships and resource selection among forest patches, the probability of forest patches being occupied by hornbills, and developed spatially explicit habitat model (SEHM) to predict probability of Sumatran hornbill occurrence at broad scale. With the combination of stochastic events and habitat loss, small-bodied territorial species groups may face extirpation in the future due to dispersal limitation. Large-bodied non-territorial species had a better probability to persist in fragmented landscapes. Application of spatially explicit modeling has great potential to fill a knowledge gap for hornbill conservation priorities at broad scales. Evaluating efficiency of conservation research and management are recommended for future hornbill studies. Maintaining remnant forest patches in proximity to large neighborhood forest complexes is imperative for future hornbill persistence.

INDEX WORDS: AIC, *Anorrhinus galeritus*, *Antracoceros albirostris*, *Antracoceros malayanus*, *Aceros corrugatus*, *Berenicornis comatus*, *Buceros rhinoceros*, *Buceros bicornis*, Distribution, Forest fragmentation, Hornbill conservation, Indonesia, Logistic regression, Occupancy estimates, Patch occupancy, Sumatran hornbills, Sumatra, *Rhinoplax vigil*, *Rhyticeros undulatus*, Spatial explicit model, detection probability

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CHAPTER 1

INTRODUCTION AND STUDY SITE

INTRODUCTION

During the last 20 years, the island of Sumatra has experienced some of the highest rates of deforestation in the world (e.g. Laurance 1999, Holmes 2001). During 1985 – 1997, 6.7 million ha of forest were lost (FWI/GFW 2002) and all major protected areas on the island were impacted (Kinnaird et al. 2003, Linkie et al. 2004, Gaveau et al. 2007). The World Bank (2001) reported that Lampung Province has the second highest deforestation rate of any Sumatra province, with approximately 44% of forest cover lost over the last 12 years. There, the average forest size has declined by a factor of four, and the number of fragments has doubled (Hadiprakarsa et al. 2007). Today, Lampung Province is the most densely human-populated and the poorest province in Sumatra (188 people/km²; data from Indonesia's Central Bureau of Statistics 2000); burgeoning human populations and the coincident deforestation continue to eliminate wildlife habitat, and what remains is highly fragmented.

Hornbills (Family Bucerotidae) are the most widespread, large, frugivorous birds in the Old World tropics (Kemp 1995). Indonesia is home for 13 hornbill species, making this country the richest and the most important country for hornbill conservation in Asia. With 9 species, the second largest island of Sumatra is the most diverse hornbill island in the country and in Asia realm. Sumatran hornbills inhabit lowland to mountain evergreen rainforest at elevations up to 1800 m, but most are commonly found in the primary, lowland evergreen rainforest (MacKinnon et al. 1993, Table 1.1). In southern Sumatra, Lampung province, most of the remnant forest

patches are occupied by hornbills with at least one species found in most forest patches (Hadiprakarsa et al. 2007). The largest forest patch in the landscape, Bukit Barisan Selatan National Park (BBSNP), holds most of the hornbill species.

The Indonesia Government has provided legal protection to the entire hornbill family in Indonesia (Noerdjito and Maryanto 2001). The IUCN has listed nearly half of Indonesian hornbills as Threatened and one considered Vulnerable; the main threats are habitat loss, habitat fragmentation and hunting (IUCN 2007). Most of common species have been studied with at least some aspects of their biology investigated. However, much of this information comes from Thailand (e.g. Tsuji et al. 1987, Poonswad et al. 1988, Kanwatanakid-Savini and Poonswad 2007). In Indonesia, a few studies of hornbills were conducted in Kalimantan and Sulawesi (e.g. Leighton 1982, Suryadi et al. 1998, Kinnaird and O'Brien 1999). However, there are still information gaps for hornbill species in Sumatra and studies are limited to the 4 common species (Anggraini et al. 2001, Hadiprakarsa and Kinnaird 2004, Hadiprakarsa et al. 2007). Detailed status and distribution of hornbills, breeding biology, demographic studies, movement patterns and dispersal are generally unavailable for most of the species (Kinnaird and O'Brien 2007). Therefore, this gap in data makes it difficult for management and conservation of these species.

From desert arid regions of Africa to tropical rainforest in Asia, hornbills play unique roles in the folklore and rituals in many human cultures. There are also economical and political implications of hornbill conservations (Kemp 1995, Kinnaird and O'Brien 2007). Hornbill body parts, such as tail feathers, heads and casques are used as costume ornamentation for cultural ceremonies (Kinnaird and O'Brien 2007). In Asia, at least two-thirds of hornbill species have been hunted and exploited for consumption (Bennett 2000, Johnson et al. 2003, Setha 2004, Datta 2007, Oliver and Wilkinson 2007). TRAFFIC Southeast Asia has only reported a few

records of hornbills as part of the pet trade in Sumatra during 1997-2001 (Sheperd et al. 2004). However, this information was reported for only a single province in west Sumatra, therefore hunting and trade of Sumatra hornbills occur at unknown rates (Y. Hadiprakarsa, *personal observation*).

Asian hornbills are large-bodied species, ranging from 0.5 to 2.5 kg (Kemp 1995) and are highly frugivorous (Kinnaird et al. 1996, Hadiprakarsa and Kinnaird 2004). Hornbills are capable of moving long distances to search for fruit resources that are patchily distributed and fluctuate over time (Tsuji et al. 1987, Suryadi et al. 1998, Holbrook et al. 2002). Hornbill studies in Asia (Kinnaird 1998) and Africa (Holbrook and Smith 2000) have found that hornbills are very effective in dispersing seeds, thus it has been suggested that hornbills may play important ecological roles in forest regeneration. To fulfill their energy requirements, hornbills rely heavily on fruit and a small number of small vertebrates and invertebrates in their diet. Food habit studies on various hornbills in Asia showed that figs (*Ficus* spp.) comprise 69% to 98% of their overall diet (Poonswad et al. 1983, Kinnaird et al. 1996, Datta and Rawat 2003, Hadiprakarsa and Kinnaird 2004). However, their diet may change slightly during the breeding season to adjust nutrient supplies for chick development (Poonswad et al. 2004).

Hornbills are secondary cavity nesting birds, and are excavate to unearth their own nest cavities. A previous study found that suitable natural cavities for hornbill nests are commonly found within large trees with a diameter at breast height (DBH) over 65 cm (Poonswad et al. 2000, Cahill 2003). Therefore, availability of suitable tree cavities is a key factor for maintaining hornbill populations (Kemp 1995). Synthesizing from numerous hornbill studies in Asia, there are 3 indispensable features required for hornbill persistence: 1) ample food resources, 2) an adequate number of large trees with suitable nest cavities for hornbills to breed,

and 3) sufficient habitat area to support viable populations. These critical components of their natural history make them susceptible to fragmentation of tropical forest (Terborgh and Winter 1980, Lambert 1992, Datta 1998, Anggraini et al. 2001), and also to reduction in quality of forest habitats (Kinnaird and O'Brien 2007).

With increasing tropical forest loss and isolation of remaining forest patches, persistence of forest species is likely to be dependent on their ability to persist in fragmented landscapes. Island biogeography theory (MacArthur and Wilson 2001) and metapopulation theory (Levins 1969) have provided a conceptual basis for evaluating the contributions of colonization and extinction of wildlife in a fragmented landscape. Several studies have suggested that forest fragmentation can affect bird community richness (e.g. Telleria et al. 2003, Sodhi et al. 2005), distribution (e.g. Waltert et al. 2004, Veech 2006), abundance (e.g. Lampila et al. 2005, Stouffer et al. 2006), forest occupancy (e.g. Villard et al. 1999, Gibson et al. 2004) and in extreme cases, can lead to species extinction (e.g. Newmark 1991, Castelletta et al. 2000). Most of the major fragmentation studies have come from the Neotropics and have concentrated on understory and small-bodied bird species in relatively few forest patches (e.g. McGarigal and McComb 1995, Stouffer and Bierregaard 1995, Christiansen and Pitter 1997, Lee et al. 2002). However, there is a paucity of studies on the effects of fragmentation on large, canopy-dwelling (Galletti 1996) and wide-ranging bird species, especially those in the Asian tropics (Laurance and Bierregaard 1997).

Hornbill populations may be able to persist in small forest patches and disturbed habitats in a landscape (Datta 1998, O'Brien et al. 1998, Raman and Mudappa 2003, Sitompul et al. 2004), but this ability likely varies among species according to habitat needs, landscape configurations, and dispersal abilities. Few studies have directly addressed the effects of habitat

fragmentation at the landscape level on Asian hornbills; most have mainly considered the impact on one or two species in predominantly forested landscapes. A study on the effect of forest fragmentation on hornbill communities in southern Sumatra (Hadiprakarsa et al. 2007) found that forest patch size is important to maintain the hornbill community, specifically for large bodied and wide ranging hornbill species. Previous studies in India (Raman and Mudappa 2003), Thailand (Pattनाविbool and Dearden 2002) and Sumba, Indonesia (Sitompul et al. 2004) reported similar results. Therefore, more understanding of the effect of anthropogenic habitat change on distribution and occupancy patterns of hornbills is a prerequisite to their habitat conservation and management.

Conserving hornbills and their habitat in fragmented landscapes must include understanding and application of biological studies, and integration with conservation action. Each species has a specific habitat requirements (Wiens 1989). Identifying key habitat variables with their spatial arrangement to which a species responds, and developing habitat models to predict species occupancy, are important tools to develop species conservation plans (Gibson et al. 2004, MacKenzie 2006) and for landscape conservation planning (Sanderson et al. 2002).

Many ecological studies have been done using species occurrences to model habitat relationships (e.g., Donovan and Flather 2002, Gibson et al. 2004, Moore and Swihart 2005), resources selection (MacKenzie 2006), and estimating colonization and local extinction from site occupancy (MacKenzie et al. 2003). However, collecting such information without taking detection probability into account could lead to a seriously biased result (MacKenzie et al. 2006). Several studies have shown that imperfectly detecting species is a common problem in many wildlife studies (MacKenzie et al. 2006). Recently, MacKenzie et al. (2006) developed a likelihood-based method for estimating the proportion of area (patch) occupied when species are

detected imperfectly and detection probability varies among species or habitats. Here, species detection probability is defined as the probability of detecting at least one individual of the species during a particular sampling occasion. With careful use, applications of this method provide biologists with a better and more efficient utilization of collection data.

The major goal of this research was to assess patch occupancy characteristics of hornbills in Lampung province and to assess spatial and environmental characteristics important in predicting hornbill community persistence in forest patches, thereby extending the initial work of Hadiprakarsa et al. (2007).

The first objective of this study was to identify habitat relationships and resource selection among Sumatran hornbill species. I describe the best habitat parameters to predict hornbill occupancy in a fragmented landscape in Chapter 2.

Second, I performed a spatial modeling exercise to predict probability of occurrences for Sumatran hornbills at a broad scale. In Chapter 3, I develop spatially explicit habitat models (SEHM) of four Sumatran hornbills to predict probability of occurrence as an approach to identify habitat requirement at broad scales that can provide an alternative management tool for hornbill conservation in a fragmented landscape in southern Sumatra, Indonesia.

STUDY SITE

The study was conducted in the Southern Sumatra landscape, encompassing approximately 3.5 million ha of land and stretching across the province of Lampung and a small portion in Bengkulu province, Sumatra (3°45'S and 103°40'E, Figure 1). The topographical gradient ranges from gentle slopes (<16.5°) to steep slopes (> 16.5°), with elevation from 0 to 2200 m above sea level. Forest type varied from lowland to montane dipterocarp forest. The annual rainfall is generally high, ranging between 2000–4000 mm and temperature ranges from

20–34° Celsius, although there can be severe droughts during El Niño Southern Oscillation phenomena (Hedges et al. 2005). Lampung province contains 2 large and important protected areas, Bukit Barisan Selatan National Park (BBSNP) and Way Kambas National Park (WKNP). These two national parks serve as a major wildlife refuges for a number of charismatic and endangered mammals species, such as Sumatra tiger (*Panthera tigris*), Asian elephant (*Elephas maximus*), Sumatran rhino (*Dicerorhinus sumatrensis*) (Foose and van Strien 1997, Franklin et al. 1999), and more than 200 species of birds (van Marle and Voous 1988, Y. Hadiprakarsa *unpublished data*).

Between the late 1950s and 1989, much of Lampung's forest was cleared as part of the Indonesian Government's Transmigration Program. This government program moved people from Java to Sumatra in large numbers. By 1981, 60% of the population of southern Sumatra consisted of transmigrants. This was followed by a period of spontaneous migration of people leaving the overcrowded, neighboring island of Java (Benoit et al. 1989). In the 1980s, 30 native forest patches existed in Lampung province ranging in size from 452 ha to 205,440 ha. However, by 2000s, as much as 35% of forest cover was lost, and several patches present in the 1980s had disappeared (Hadiprakarsa et al. 2007). Remnant forest patches in 2000 were dominated by lowland evergreen forest (<500 msl) to hill forest areas (1000 msl). These patches were surrounded by dense human settlement, plantations and an agricultural matrix. Most of forest loss in the landscape occurred in the outside of two national parks (Gaveau et al. 2007) and was primarily caused by illegal logging and agricultural practices, such as coffee plantation (Kinnaird et al. 2003, Gaveau et al. 2007).

LITERATURE CITED

- Anggraini, K., M. F. Kinnaird, and T. G. O'Brien. 2001. The effects of fruit availability and habitat disturbance on an assemblage of Sumatran hornbills. *Bird Conservation International* 10:189-202.
- Bennett, E. L. 2000. Saving Borneo's bacon: The sustainability of hunting in Sarawak and Sabah. Pages 305-324 in J. G. Robinson, and E. L. Bennett, editors. Columbia University Press, New York.
- Benoit, D., P. Levang, M. Pain, and O. Sevin. 1989. Transmigration et migrations spontanées en Indonésie: Propinsi Lampung. Departemen Transmigrasi, Jakarta, Indonesia and ORSTOM, Bondy, France.
- Cahill, A. J. 2003. Nest-site characteristics of the Red-knobbed Hornbill *Aceros cassidix* and Sulawesi Dwarf Hornbill *Penelopides exarhatus*. *Ibis* 145:E97-E113.
- Castelletta, M., N. S. Sodhi, and R. Subaraj. 2000. Heavy Extinctions of Forest Avifauna in Singapore: Lessons for Biodiversity Conservation in Southeast Asia. *Conservation Biology* 14:1870-1880.
- Christiansen, M. B., and E. Pitter. 1997. Species loss in a forest bird community near Lagoa Santa in southeastern Brazil. *Biological Conservation* 80:23-32.
- Datta, A. 1998. Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. *Oryx* 32:285-294.
- _____. 2007. Hunting for hornbills: approaches to conservation in Arunachal Pradesh, north-east India. Pages 41 in *Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4th International Hornbill Conference, Mabula Game Lodge, Bela- Bela, South Africa.*

- Datta, A., and G. S. Rawat. 2003. Foraging Patterns of Sympatric Hornbills during the Nonbreeding Season in Arunachal Pradesh, Northeast India. *BIOTROPICA* 35:208-218.
- Donovan, T., and C. Flather. 2002. Relationships among north American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* 12:364-374.
- Foose, T. J., and N. van Strien. 1997. Asian Rhinos - Status survey and conservation action plan. IUCN, Gland, Switzerland and Cambridge, UK.
- Franklin, N., Bastoni, Sriyanto, D. Siswomartono, J. Manansang, and R. Tilson. 1999. Last of the Indonesian tigers: a causes for optimism. Pages 130-147 *in* J. Seidensticker, S. Christie, and P. Jackson, editors. *Riding the tiger: Tiger Conservation in Human-dominated Landscapes*. Cambridge University Press, Cambridge, UK.
- FWI/GFW. 2002. The State of the Forest: Indonesia. Forest Watch Indonesia, Bogor, Indonesia and Global Forest Watch, Washington, DC.
- Galleti, M. 1996. Fruits and frugivores in a Brazilian Atlantic Forest. University of Cambridge, U.K.: Unpublished Ph.D. thesis. .
- Gaveau, D. L. A., H. Wandono, and F. Setiabudi. 2007. Three decades of deforestation in southwest Sumatra: Have protected areas halted forest loss and logging, and promoted re-growth? *Biological Conservation* 134:495-504.
- Gibson, L., B. Wilson, D. Cahill, and J. Hill. 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *Journal of Applied Ecology* 41:213-223.
- Hadiprakarsa, Y., and M. F. Kinnaird. 2004. Foraging characteristics of an assemblage of four Sumatran hornbill species. *Bird Conservation International* 14:S53-S62.
- Hadiprakarsa, Y., M. F. Kinnaird, M. Iqbal, and T. G. O'Brien. 2007. Effects of forest fragmentation on hornbills across the southern Sumatran landscape. Pages 80-91 *in*

- Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4th International Hornbill Conference. Mabula Game Lodge, Bela-Bela, South Africa.
- Hedges, S., M. J. Tyson, A. F. Sitompul, M. F. Kinnaird, and D. Gunaryadi. 2005. Distribution, status, and conservation needs of Asian elephants (*Elephas maximus*) in Lampung Province, Sumatra, Indonesia. *Biological Conservation* 124:35-48.
- Holbrook, K. M., and T. B. Smith. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* 125:249-257.
- Holbrook, K. M., T. B. Smith, and B. D. Hardesty. 2002. Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* 25:745-749.
- Holmes, D. A. 2001. Deforestation in Indonesia: A Review of the Situation in Sumatra, Kalimantan, and Sulawesi. World Bank. Jakarta, Indonesia.
- IUCN. 2007. 2007 IUCN Red List of Threatened Species On the World Wide Web: <http://www.redlist.org> (Accessed on 22 October 2007)
- Johnson, A., M. Singh, Dongdala, and O. Vongsa. 2003. Wildlife hunting and use in the Nam Ha national protected area: Implications for rural livelihoods and biodiversity conservation. Vientisnr, Lao PDR: Wildlife Conservation Society.
- Kanwatanakid-Savini, C., and P. Poonswad. 2007. Feeding ecology and food selection of four sympatric hornbill species at Khao Yai National Park, Thailand. Pages 195 *in* Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4th International Hornbill Conference. Mabula Game Lodge, Bela-Bela, South Africa.

- Kemp, A. 1995. *The Hornbills*. Oxford University Press Oxford.
- Kinnaird, M., and T. G. O'Brien. 2007. *The Ecology and Conservation of Asian Hornbills: Farmers of the Forest*. The University of Chicago Press, Chicago.
- Kinnaird, M. F. 1998. Evidence for Effective Seed Dispersal by the Sulawesi Red-Knobbed Hornbill, *Aceros cassidix*. *BIOTROPICA* 30:50-55.
- Kinnaird, M. F., and T. G. O'Brien. 1999. Breeding ecology of the Sulawesi Red-Knobbed Hornbill *Aceros cassidix*. *Ibis* 141:60-69.
- Kinnaird, M. F., T. G. O'Brien, and S. Suryadi. 1996. Population fluctuation in Sulawesi Red-knobbed Hornbills: tracking figs in space and time. *Auk* 113:431-440.
- Kinnaird, M. F., E. W. Sanderson, T. G. O'Brien, H. T. Wibisono, and G. Woolmer. 2003. Deforestation Trends in a Tropical Landscape and Implications for Endangered Large Mammals. *Conservation Biology* 17:245-257.
- Lambert, F. R. 1992. The Consequences of Selective Logging for Bornean Lowland Forest Birds. *Philosophical Transactions: Biological Sciences* 335:443-457.
- Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic Responses by Birds to Forest Fragmentation. *Conservation Biology* 19:1537-1546.
- Laurance, W. F. 1999. Reflections on the tropical deforestation crisis. *Biological Conservation* 91:109-117.
- Laurance, W. F., and R. O. Bierregaard. 1997. *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago.
- Lee, M., L. Fahrig, K. Freemark, and D. Currie. 2002. Importance of patch scale vs landscape scale on selected forest birds. *Oikos* 96:110-118.

- Leighton, M. 1982. Fruit Resources and Patterns of Feeding, Spacing and Grouping Among Sympatric Bornean Hornbills (Bucerotidae). PhD Dissertation, University of California, Davis.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*:237-240.
- Linkie, M., R. J. Smith, and N. Leader-Williams. 2004. Mapping and predicting deforestation patterns in the lowlands of Sumatra. *Biodiversity and Conservation* 13:1809-1818.
- MacArthur, R. H., and E. O. Wilson. 2001. *The theory of island biogeography*. Princeton University Press Princeton, NJ.
- MacKenzie, D. I. 2006. Modeling the Probability of Resource Use: The Effect of, and Dealing with, Detecting a Species Imperfectly. *Journal of Wildlife Management* 70:367-374.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating Site Occupancy, Colonization, and Local Extinction when a Species is Detected Imperfectly. *Ecology* 84:2200-2207.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines, editors. 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, San Diego, USA.
- MacKinnon, J., K. Phillipps, P. Andrew, and F. Rozendaal. 1993. *A field guide to the birds of Borneo, Sumatra, Java, and Bali*. Oxford University Press, Oxford.
- McGarigal, K., and W. C. McComb. 1995. Relationships Between Landscape Structure and Breeding Birds in the Oregon Coast Range. *Ecological Monographs* 65:235-260.

- Moore, J. E., and R. K. Swihart. 2005. Modeling patch occupancy by forest rodents: Incorporating detectability and spatial autocorrelation with hierarchically structured data. *Journal of Wildlife Management* 69:933-949.
- Newmark, W. D. 1991. Tropical fragmentation and the extinction of understorey birds in the Eastern Usambara mountains. *Conservation Biology* 5:67-78.
- Noerdjito, M., and I. Maryanto. 2001. Jenis-jenis hayati yang dilindungi perundang-undangan Indonesia (In Indonesian). Balitbang Zoologi (Museum Zoologicum Bogoriense) Puslitbang Biologi-LIPI and The Nature Conservancy, Bogor.
- O'Brien, T. G., M. F. Kinnaird, P. Jepson, and I. Setiawan. 1998. Effect of forest size and structure on the distribution of Sumba Wreathed Hornbills *Aceros everetti*. Pages 209-217 in *Proceedings of The Asian Hornbills: Ecology and Conservation, Proceedings of the Second Asian Hornbill Workshop, Bangkok*.
- Oliver, W. L. R., and R. Wilkinson. 2007. Philippine hornbills conservation programme. Pages 13-30 in *Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4 International Hornbill Conference, Mabula Game Lodge, Bela- Bela, South Africa*.
- Pattanaibool, A., and P. Dearden. 2002. Fragmentation and wildlife in montane evergreen forests, northern Thailand;. *Biological Conservation* 107:155-164.
- Poonswad, P., V. Chimchome, K. Plongmai, and P. Chuailua. 2000. Factors influencing the reproduction of Asian Hornbills. Pages 1740-1755 in *Proceedings of the 22nd International Ornithological Congress, Durban*.

- Poonswad, P., a. Tsuji, and N. Jirawatkavi. 2004. Estimation of nutrients delivered to nest inmates by four sympatric species of hornbills in Khao Yai National Park, Thailand. *ORNITHOLOGICAL SCIENCE* 3:99-112.
- Poonswad, P., A. Tsuji, and C. Ngarmpongsai. 1983. A study of the breeding biology of hornbills (Bucerotidae) in Thailand. Pages 239-265 *in* Proceedings of a Delacour/International Foundation for the Conservation of Birds in Captivity.
- _____. 1988. A comparative ecological study of four sympatric hornbills (Family Bucerotidae) in Thailand. *Acta XIX congressus Internationalis Ornithologi* 2:2781-2791.
- Raman, T., and D. Mudappa. 2003. Correlates of hornbill distribution and abundance in rainforest fragments in the southern Western Ghats, India. *Bird Conservation International* 13:199-212.
- Sanderson, E. W., K. H. Redford, A. Vedder, P. B. Coppolillo, and S. E. Ward. 2002. A conceptual model for conservation planning based on landscape species requirements. *Landscape and Urban Planning* 58:41-56.
- Setha, T. 2004. The status and conservation of hornbills in Cambodia. *Bird Conservation International* 14:S5-S11.
- Sheperd, C. R., J. Sukumaran, and S. A. Wich. 2004. Open season: An analysis of the pet trade in Medan, Sumatra 1997-2001. *TRAFFIC Southeast Asia*. Petaling Jaya, Selangor Malaysia.
- Sitompul, A. F., M. F. Kinnaird, and T. G. O'Brien. 2004. Size matters: the effects of forest fragmentation and resource availability on the endemic Sumba Hornbill *Aceros everetti*. *Bird Conservation International* 14:S23-S37.

- Sodhi, N. S., T. M. Lee, L. P. Koh, and R. R. Dunn. 2005. A century of avifaunal turnover in a small tropical rainforest fragment. *Animal Conservation* 8:217-222.
- Stouffer, P. C., and R. O. Bierregaard. 1995. Use of Amazonian Forest Fragments by Understory Insectivorous Birds. *Ecology* 76:2429-2445.
- Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy. 2006. Long-Term Landscape Change and Bird Abundance in Amazonian Rainforest Fragments. *Conservation Biology* 20:1212-1223.
- Suryadi, S., M. F. Kinnaird, and T. G. O'Brien. 1998. Home ranges and daily movements of the Sulawesi red-knobbed hornbill *Aceros cassidix* during the non-breeding season. Pages 159-170 *in* Proceedings of The Asian hornbills: ecology and conservation. Thai Studies in Biodiversity.
- Telleria, J. L., R. Baquero, and T. Santos. 2003. Effects of forest fragmentation on European birds: implications of regional differences in species richness. *Journal of Biogeography* 30:621-628.
- Terborgh, J., and B. Winter. 1980. Some causes of extinction Pages 119-113 *in* M. E. Soule, and B. A. Wilcox, editors. *Conservation biology: An Evolutionary-Ecological Perspective*. Sinauer, Sunderland, Massachusetts.
- Tsuji, A., P. Poonswad, and N. Jirawatkari. 1987. Application of radio tracking to study ranging pattern of hornbills (Bucerotidae) in Thailand. Pages 316-351 *in* Proceedings of Proceedings of the Jean Delacour/International Foundation for the Conservation of Birds Symposium on Breeding Birds in Captivity.

- UNEP-WCMC. 2007. UNEP-WCMC Species Database: CITES-Listed Species On the World Wide Web: <http://www.cites.org/eng/resources/species.html> (Accessed on 22 October 2007)
- van Marle, J. G., and K. H. Voous. 1988. The birds of Sumatra: an annotated check-list. Pages 1-265 *in* British Ornithological Union Check-list 10. British Ornithological Union, Tring, UK.
- Veech, J. A. 2006. Increasing and Declining Populations of Northern Bobwhites Inhabit Different Types of Landscapes. *Journal of Wildlife Management* 70:922-930.
- Villard, M.-A., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation Effects on Forest Birds: Relative Influence of Woodland Cover and Configuration on Landscape Occupancy. *Conservation Biology* 13:774-783.
- Waltert, M., A. Mardiasuti, and M. Muhlenberg. 2004. Effects of Land Use on Bird Species Richness in Sulawesi, Indonesia. *Conservation Biology* 18:1339-1346.
- Wiens, J. A. 1989. Spatial Scaling in Ecology. *Functional Ecology* 3:385-397.
- World Bank. 2001. Indonesia: Environment and Natural Resource Management in a Time of Transition. The World Bank. Washington D.C.

Table 1.1. Common names, scientific names and current conservation status of hornbills occurring in Sumatra, Indonesia.

| Scientific Name ¹ | Common Name ¹ | Weight/ranging pattern ² | Conservation Status | | |
|----------------------------------|--------------------------|-------------------------------------|---------------------|-------------------|--------------------|
| | | | INDO ³ | IUCN ⁴ | CITES ⁵ |
| <i>Berenicornis comatus</i> | White-crowned Hornbill | 1.3 – 1.4 kg/Territorial | P | NT | II |
| <i>Aceros corrugatus</i> | Wrinkled Hornbill | 1.3 – 1.6 kg/Non-territorial | P | NT | I |
| <i>Rhyticeros undulatus</i> | Wreathed Hornbill | 1.9 – 2.5 kg/Non-territorial | P | LC | II |
| <i>Buceros bicornis</i> | Great-pied Hornbill | 2.6 – 3.4 kg/Non-territorial | P | NT | I |
| <i>Buceros rhinoceros</i> | Rhinoceros Hornbill | 2 – 2.9 kg/Non-territorial | P | NT | II |
| <i>Rhinoplax vigil</i> | Helmeted Hornbill | 2.5 – 3.1 kg/Non-territorial | P | NT | I |
| <i>Anorrhinus galeritus</i> | Bushy-crested Hornbill | 0.9 – 1.2 kg/Territorial | P | LC | II |
| <i>Anthracoceros albirostris</i> | Oriental Pied Hornbill | 0.6 – 0.7 kg/Territorial | P | LC | II |
| <i>Anthracoceros malayanus</i> | Malay Black Hornbill | 0.6 – 1 kg/Territorial | P | NT | II |

¹Kemp (2001), ² Kemp (1995), ³Indonesia Natural Resources Act No. 5, 1990 and Indonesia Government Regulation No. 7, 1999; ⁴

International Union for Conservation of Nature and Natural Resources (IUCN) 2007. ⁵ United Nations Environment Programme-

World Conservation Monitoring Centre (UNEP-WCMC) 2007. Abbreviation: P= Protected; NT=Near threatened; LC=Least concern;

I and II, appendices in Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

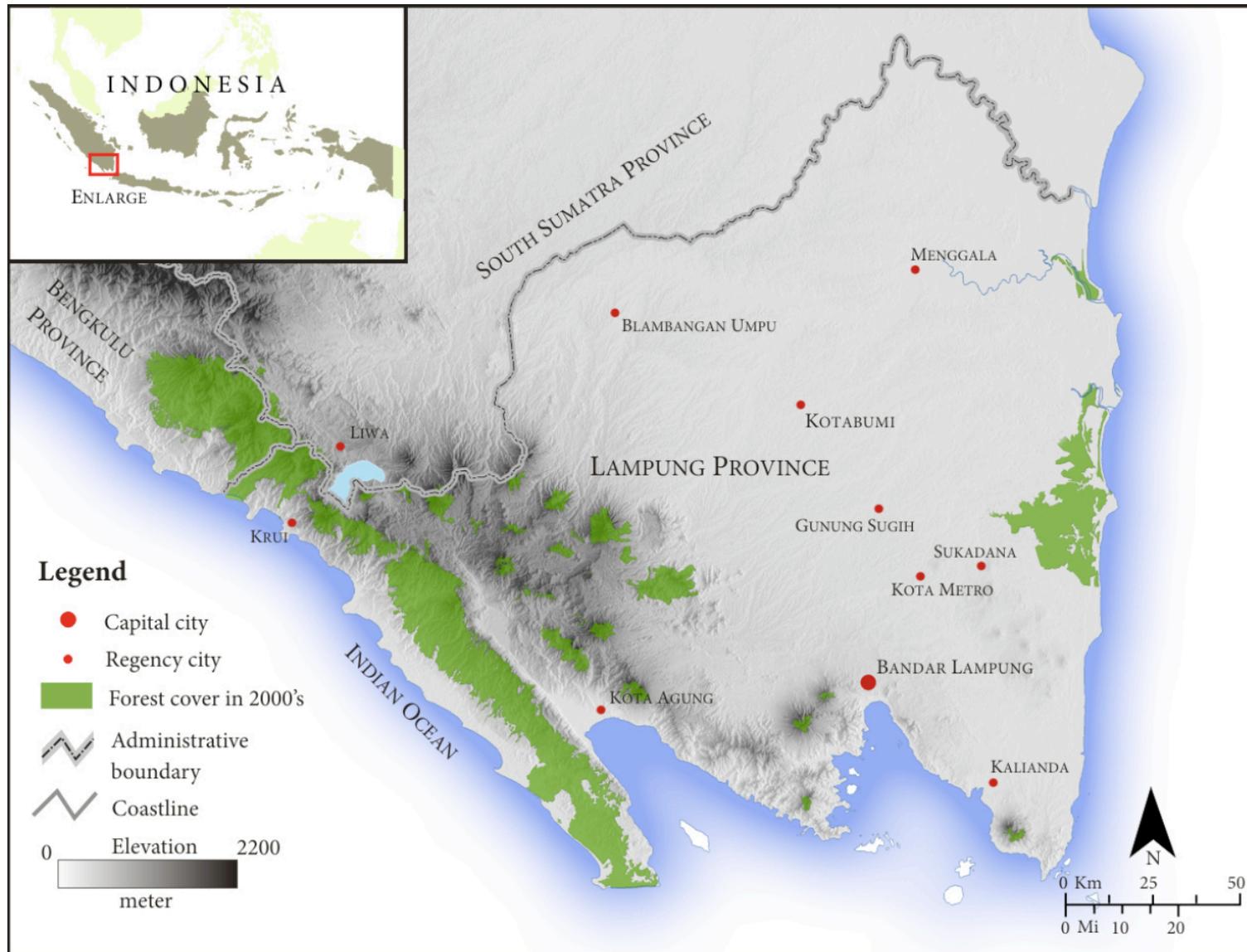


Figure 1.1. Location of Lampung Province, Sumatra, Indonesia.

CHAPTER 2

RELATIONSHIP OF HABITAT AND RESOURCE SELECTION TO SUMATRAN HORNBILL PATCH OCCUPANCY IN SOUTHERN SUMATRA, INDONESIA¹

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ABSTRACT

Globally, Asian hornbill persistence is under fire due to habitat destruction by anthropogenic causes. The ability of hornbills to persist in the landscape is species-specific with respect to resource availability, habitat quality and landscape configuration. However, which environmental variables are cues for hornbills to occupy forest patches are still unknown. We investigated the relationship between habitat and resources to the probability of forest patches being occupied by Sumatran hornbills. Our results indicate positive relationships of resources availability, habitat characteristics, and landscape characteristics to the probability of a patch being occupied by seven Sumatran hornbills and their detection probability. The large-bodied non-territorial species appeared to be more flexible to occupied forest patches in fragmented landscape. In addition, fruit resources were an important covariate to their proportion of patches occupied. For small-bodied territorial species, availability of large trees as potential nest trees was more important to their patch occupancy. Probability of patch occupancy was higher on low disturbance forest patches for four hornbill species. Forest patch size was an important covariate to estimate probability of patch occupied for at least five species of hornbills. In general, patch isolation appeared to not have a strong affect as a covariate to estimate patch occupancy for hornbills.

INTRODUCTION

Habitat characteristics and resource availability exert a strong influence on bird communities and each species within the community has specific requirements (e.g., Wiens et al. 1987, Wiens 1992). The relationship between wildlife species and their habitats has been a central issue in conservation biology studies as one of an information input for conservation planning (e.g. Gu and Swihart 2004, MacKenzie et al. 2006). Identifying key habitat variables

with their spatial arrangement to which a species responds and habitat modeling to predict species occupancy are important to develop conservation management plans for species (Gibson et al. 2004, MacKenzie 2006) and for landscape conservation planning (Sanderson et al. 2002). From empirical evidence, distribution and abundance, or at least occupancy of species, are influenced by a number of factors including habitat quality (e.g., Sieving and Karr 1997, Watson et al. 2004) and resource availability (e.g., Blake and Loiselle 1991, Kinnaird et al. 1996, Telleria et al. 2003). However, when habitats become fragmented, these processes may add complexity by taking account spatial arrangement of fragments must be incorporated into the process (Villard et al. 1999, Radford and Bennett 2007).

Many ecological studies have been done using species occurrences to model habitat relationships (e.g., Donovan and Flather 2002, Gibson et al. 2004, Moore and Swihart 2005, MacKenzie 2006). However, this approach could lead to a serious bias due to the imperfect detection of the target species (MacKenzie et al. 2006). Consequently, falsely predicting species absence may be a potential source of error (Gu and Swihart 2004). Recently, MacKenzie et al. (2006) developed a likelihood-based method for estimating the proportion of an area (patch) occupied when the species are detected imperfectly and detection varies among species or habitats.

Habitat fragmentation is a process through which a focal habitat type is partially or completely removed, thereby altering its original configuration. Combination of the effects of fragmentation, habitat loss and changes in configuration can potentially reduce population persistence in a landscape (Villard et al. 1999). Many empirical studies suggest that forest fragmentation can negatively effect forest bird community richness (e.g. Telleria et al. 2003, Sodhi et al. 2005), distribution (e.g. Waltert et al. 2004, Veech 2006), abundance (e.g. Lampila et

al. 2005, Stouffer et al. 2006), forest occupancy (e.g. Villard et al. 1999, Gibson et al. 2004), and in extreme cases lead to species extinction (e.g. Newmark 1991, Castelletta et al. 2000). Most of the forest fragmentation studies on birds have come from the Neotropics and have concentrated on understory and small-bodied species in relatively few forest patches (e.g. McGarigal and McComb 1995, Stouffer and Bierregaard 1995, Christiansen and Pitter 1997, Lee et al. 2002). However, there is a paucity of studies on the effects of fragmentation on large, canopy-dwelling (Galleti 1996), and wide-ranging species, especially those in the Asian tropics (Laurance and Bierregaard 1997).

During the last 20 years, the island of Sumatra has experienced some of the highest rates of deforestation in the world (e.g. Laurance 1999, Holmes 2001). During 1985 – 1997, 6.7 million ha of forest were lost (FWI/GFW 2002) and all major protected areas on the island were affected (Kinnaird et al. 2003, Linkie et al. 2004, Gaveau et al. 2007). The World Bank (2001) reported that Lampung Province had the second highest deforestation rate of any Sumatra province, with approximately 44% of forest cover lost over the last 12 years. There, average forest size has declined by a factor of four, and the number of fragments has doubled (Hadiprakarsa et al. 2007). Today, Lampung Province is the most densely human-populated and the poorest province in Sumatra (191 people/km²; data from Indonesia's Central Bureau of Statistic 2000); burgeoning human populations and the coincident deforestation continue to eliminate habitat, and what remains is highly fragmented (Hadiprakarsa et al. 2007).

Indonesia is a home for 13 hornbill (Order Coraciiformes, Family: Bucerotidae) species, making this country the richest and the most important country for hornbill conservation in Asia (Kinnaird and O'Brien 2007). With nine species, the second largest island, Sumatra, is the most diverse hornbill island in the country and in the Asia realm. Sumatran hornbills inhabit lowland

to mountain evergreen rainforest at elevations up to 1800 m, but most are commonly found in the primary, lowland evergreen rainforest (MacKinnon et al. 1993), Table 1). In Indonesia, few hornbill studies were conducted in Kalimantan and Sulawesi (e.g. Leighton 1982, Suryadi et al. 1998, Kinnaird and O'Brien 1999). However, there are still information gaps for hornbill species in Sumatra and existing information is limited to the 4 common species (Anggraini et al. 2001, Hadiprakarsa and Kinnaird 2004, Hadiprakarsa et al. 2007). Conversely, detailed status and distribution of hornbills, breeding biology, demographic studies, movement patterns and dispersal are generally unavailable for most of the species (Kinnaird and O'Brien 2007). Therefore, this knowledge gap makes it difficult to setup management and conservation priorities of these species.

Asian hornbills are large-bodied species and are highly frugivorous (0.5 to 2.5 kg) (Kinnaird et al. 1996, Hadiprakarsa and Kinnaird 2004). To fulfill their energy requirements, hornbills rely heavily on fruit and a small number of small vertebrates and invertebrates in their diet. Although nearly 500 fruit species are eaten by Asian hornbills, figs (*Ficus* spp.) comprise a large proportion with an average of 69% to 98% of their overall diet (Poonswad et al. 1983, Kinnaird et al. 1996, Datta and Rawat 2003, Hadiprakarsa and Kinnaird 2004). Their diet may change slightly during the breeding season to adjust nutrient supplies for chick development (Poonswad et al. 2004). In search of fruit resources that are patchily distributed, hornbills are capable of traveling long distances (Tsuji et al. 1987, Suryadi et al. 1998, Holbrook et al. 2002). Hornbill studies in Asia (Kinnaird 1998) and Africa (Holbrook and Smith 2000) have found that hornbills are very effective in dispersing seeds, thus it has been suggested that hornbills are critical agents of rain forest regeneration by dispersing seed effectively compared with other

frugivore species (Kinnaird 1998, Holbrook and Smith 2000, Wang and Smith 2002, Kinnaird and O'Brien 2007).

Hornbills are secondary cavity nesting birds, and unable to excavate their own nest cavities. A previous study found that suitable natural cavities for hornbill nests are commonly found within large trees with a diameter at breast height over 65 cm (Poonswad et al. 2000, Cahill 2003). Numerous Asian hornbill ecological studies, in India (Kannan and James 1999, e.g., Datta 2001, Raman and Mudappa 2003), Thailand (e.g., Tsuji et al. 1987, Poonswad et al. 1988, Poonswad et al. 2000, Kanwatanakid-Savini and Poonswad 2007) and Indonesia (e.g., Leighton 1982, Kinnaird et al. 1996, Hadiprakarsa and Kinnaird 2004), showed that availability of fruit resources, availability of large trees with suitable nest cavities and primary forest that can hold their populations are three main features for hornbills to survive. However, alarming rates of forest lost, deterioration of the forest landscape, and fragmentation by anthropogenic causes has reduced current hornbill habitat in all Asia regions (Kinnaird and O'Brien 2007).

Hornbill populations may be able to persist in small forest patches and disturbed habitats in a landscape (Datta 1998, O'Brien et al. 1998, Raman and Mudappa 2003, Sitompul et al. 2004), but this ability likely varies among species according to habitat needs, landscape configurations, and dispersal abilities (Hadiprakarsa et al. 2007). In addition, when hornbills live in a fragmented landscape it is likely they are forced to occupy the existing forest patches in the landscape to maintain their persistence. However, which environmental variables, such as habitat quality or resources, are more important as a cue for hornbills to occupy a forest patch are still unknown. Extending from initial work of Hadiprakarsa et al. (2007), in this study we investigated the relationship between habitat and resources as environmental predictors to the probability of forest patches being occupied by Sumatran hornbills.

METHODS

Study area and site selections

Our study was conducted across the southern Sumatra landscape, encompassing approximately 3.5 million hectares of land and stretching across the province of Lampung and a small portion in Bengkulu province, Sumatra (3°45'S and 103°40'E, Figure 1). Topographical gradient ranges from gentle slopes (<16.5°) to steep slopes > 16.5°, with elevation from 0 – 2,200 msl. Forest type ranged from lowland to montane dipterocarp forest. Annual rainfall is generally high, ranging between 2,000 – 4,000 mm and temperature ranges from 20 – 34° Celsius, although there can be severe droughts during El Nino Southern Oscillation phenomena (Hedges et al. 2005). Lampung province contains two important protected areas, Bukit Barisan Selatan National Park and Way Kambas National Park. These two national parks serve as major wildlife refuges for a number of celebrity endangered mammals, such as Sumatra tiger (*Panthera tigris*), Asian elephant (*Elephas maximus*), and Sumatran rhino (*Dicerorhinus sumatrensis*) (Foose and van Strien 1997, Franklin et al. 1999), and more than 200 species of birds (van Marle and Voous 1988, Y. Hadiprakarsa unpublished data).

To identify remnant forest patches, land-cover analysis was carried out by the GIS Department from the Wildlife Conservation Society Indonesia Program (WCS-IP) using LANDSAT 7 ETM+ for the year 2000, which had negligible (less than 10%) cloud cover. Classification of land-cover was grouped into forest and non-forest, using a combination of unsupervised classification and manual interpretation. We define a forest patch as any closed canopy forest greater than 100 hectares and forest patch area that is greater than 50,000 hectares from 60 forest patches identified, only 34 forest patches met this criterion, with only two forest patches in the BBSNP complex that met source patches.

For each forest patch, a series of patch metric variables related to its size and isolation were quantified. We used the patch Analyst extension version 2.3 for ArcGIS 9.x (Rampel and Carr 2003) to measure patch size and size of nearest neighboring patch. Patch isolations, a metric that represents distance (in km) to the nearest neighbor patch, distance to source patch and number of patches that serve as a stepping stone to the source forest, was extracted using Nearest Features extension version 3.8 for ArcView 3.x (Jenness 2004). Since many variables were correlated across sites, we used principal component analysis (PCA) to summarize variation in the data set and identify groups of inter-correlated variables to classify forest patches for survey site selections. The PCA results grouped the forest patches into three patch size classes and two isolation categories: small (< 1,000 ha), medium (1,000 – 5,000 ha) and large (> 5,000 – 50,000 ha), and if the patch was not isolated and located close to (< 5 km) or isolated and far from (>5 km) nearest patches and the source forest. With roughly an equal number of forest patches in each size and isolation patch groups, we randomly selected 18 from the 34 forest patches to be surveyed encompassing approximately 92% of the sampling area in a landscape. Most of the surveyed forest patches were under some form of protected management status by provincial or central government, ranging from nature forest reserves to national parks. Only one small forest patch had a limited production forest status (Table 2.2).

Hornbill occupancy

Hornbills were surveyed during January to August 2003 in 18 forest patches across the landscape. We used standard line transect methods (Buckland et al. 2001) to obtain hornbill detection histories for occupancy estimation analysis. The numbers of transects walked and transect length varied according to the forest size category and accessibility (Table 2.2). Each transect was walked in the morning (0600-1000) and afternoon (1300-1700) on at least two days

for each forest patches. The detection of hornbills from visual, vocal or wing beat data, or non-detection, was recorded for each occasion.

As transects were identified and marked, we quantified hornbill resources and habitat quality within the forest adjacent to the line transects every 200 m with 15 m width on either side of the transect. To assess hornbill resources, we counted the number of reproductive-sized hemi-epiphyte fig trees (*Ficus spp.*; FIGS) and potential nest site trees, which I defined as trees with a diameter at breast height (DBH) above 45 cm. Later, We estimated density (trees/ha) on each resource parameter to be more useful for occupancy analysis. We evaluated habitat quality by looking at the level of anthropogenic habitat disturbance. We recorded occurrences of logged trees that meet criteria as potential nest site trees and occurrences of human activities indicated by cutting marks, abandoned campfires or direct encounters with humans (DIST). At each transect location, elevations (ELEV) were extracted as a global landscape covariate. In addition, two patch covariates of forest patch size (SIZE) and degree of patch isolation (ISOL) were obtained from the patch selection process. Elevation and slope data were extracted from a digital elevation model (DEM) from the NASA Shuttle Radar Topographic Mission (Rabus et al. 2003).

We used the computer program PRESENCE v.2.2 to estimate the proportion of patches occupied (PAO) and to model the factors associated with hornbill occupancy (ψ) using a likelihood-based method. This method assumes that (1) the community of species is closed to additions (immigration and colonization), deletions (emigration or extinction) or other changes during the study, (2) species are not falsely identified, and (3) the probability of detecting a species at one site is independent of the probability of detecting the species at all other sites (see MacKenzie et al. 2006). I explored the importance of covariates by modeling parameters as a logit function of habitat variables, resource availability, and landscape characteristics. All

continuous variables were standardized (Table 2.3). The set of a priori candidate models was developed based on experience and the literature. We developed a basic model that represented the spatially explicit habitat model, where occupancy (ψ) and probability of detection (p) were constant across forest patches. Potential covariates for occupancy and detection were then allowed to vary, individually or in combination, i.e. ψ (covariate) p (covariate), ψ (.) p (covariate), ψ (covariate) p (.)

Akaike's Information Criterion (AIC) values were used as the basis to rank candidate models and for model selection (Burnham and Anderson 2002). The most parsimonious model for the observed data was used to estimate hornbill occupancy. When there were a number of top ranked models with similar AIC weights model averaging was applied to estimate occupancy from multiple models for each species (Burnham and Anderson 2002), where, ω_i = AIC individual model weight and $\hat{\theta}_i$ = individual occupancy estimate:

$$\hat{\theta}_A = \sum_{l=1}^m \omega_l \hat{\theta}_l \quad (1)$$

$$S.E.(\hat{\theta}_A) = \sum_{l=1}^m \omega_l \sqrt{Var(\hat{\theta}_l | M_l) + (\hat{\theta}_l - \hat{\theta}_2)^2} \quad (2)$$

To determine which covariates were most important in predicting occupancy model, model weights were summed for all models with that particular variable (Burnham and Anderson 2002). As a result, variables with high summed weights could be considered to be more important in explaining variation in the response variable (MacKenzie et al. 2006).

RESULTS

Over 391 km were walked in 18 forest patches, all nine Sumatran hornbills were recorded with at least one species recorded in every surveyed forest patch. Overall, most species were recorded in the large forest patches with the highest number of species recorded found in source patches (Figure 2). The common hornbill species, *B. rhinoceros* and *R. undulatus* were found in 89% and 78% of the forests patches, respectively whereas *A. galeritus* was found in just over half of the forests (50%). *R. vigil* and *B. bicornis* were sighted in only 39% and 22% of the forest patches, respectively. The more elusive species, *A. albirostris*, and *A. malayanus*, were sighted only once or twice during the survey and were found only in the large and source forest patches.

Because of low sample size (< 2 detection histories) for *A. malayanus* and *A. albirostris*, only seven species were used in the analysis: *B. rhinoceros*, *B. bicornis*, *R. vigil*, *A. undulatus*, *A. corrugatus*, *B. comatus* and *A. galeritus*. In 18 forest patches, I recorded 366 hornbills on 56 transects with a varying number of sampling occasions from two to eight. However due to double detection within single occasions, only 216 hornbill occurrences were included in the analysis. The naïve estimates of occupancy varied among species. *B. rhinoceros* had the highest naïve estimate (0.61), followed by *R. undulatus*, *A. galeritus*, *R. vigil*, *B. bicornis* and *A. corrugatus* (0.45, 0.37, 0.29, 0.09, and 0.07, respectively). Also, the elusive species *B. comatus* had the lowest naïve estimate (0.04, Table 4).

Resources selection functions

The best models for each species indicated differences in occupancy rate among species with respect to fig density and potential nesting trees density (Table 2.4). Only two species had simplest models, with constant occupancy and constant detection probability, was chosen as the

top model for only two species, *R. undulatus* and *A. corrugatus* (0.661 ± 0.126 and 0.091 ± 0.049 respectively; Table 2.4).

For other species, the ‘best’ model from the set of candidate models for each species often included figs and density of potential nesting trees as important covariates for predicting occupancy. Summing Akaike weights (w) of the models revealed that, with the exception of *R. undulatus* and *A. corrugatus*, fig density and potential nesting tree density were the most important covariates for large-bodied, non-territorial species (*B. rhinoceros*, *B. bicornis* and *R. vigil*) with respect to occupancy, with summed model weight more than 50%. Potential nest tree density was the most important variable for *A. galeritus*, the only small-bodied territorial species (Figure 2.3).

Habitat relationships

Most surveyed forest patches were surrounded by a human-made matrix. Consequently, the forest interiors were subject to some level of anthropogenic disturbance such as, illegal logging, hunting, and land clearing for agriculture. We explored the importance of habitat quality and patch metrics in species-specific models. The top ranked models revealed, the importance of habitat disturbance and patch characteristics on occupancy rates for all seven-hornbill species (Table 2.5). The highest proportion of patches occupied was found for the three large-bodied and non-territorial species, *B. rhinoceros*, *R. vigil* and *R. undulatus* (Figure 2.4). For *B. rhinoceros*, probability of occupancy was related to habitat disturbance level and elevation distributions with AIC weighting (w) of 1.0 and SE = 0.05 (Table 2.5). For *R. vigil*, elevation was an important covariate with respect to species occupancy ($AIC_w = 0.66$).

Probability of patch occupancy was higher in low disturbance forest patches for *B. rhinoceros*, *B. bicornis*, *B. comatus* and *A. galeritus* (Figure 2.5). Forest patch size was an

important covariate in estimating occupancy for at least five hornbill species (Figure 2.6). In general, patch isolation did not have strong affect as on patch occupancy for hornbills. For the nomadic species, *A. undulatus*, habitat disturbance and patch size had no effects on the probability of patch occupancy (Figure. 2.5 and 2.6).

Detection probability

Patterns of detection probability with respect of resource selection and habitat relationship varied among species. Detection probabilities for large-bodied, non-territorial species were often affected by one or more landscape characteristics of patch size, elevation and patch isolation (Table 2.4 and 2.5). For two small-bodied territorial species, *B. comatus* and *A. galeritus*, detection probability was affected by patch isolation. For most of hornbill species, detection probability was high in forest patches with a high intensity of disturbance (Figure 2.5).

DISCUSSION

In this study, patch occupancy and detection probability were related to resource availability, habitat characteristics and landscape characteristics. The large-bodied non-territorial hornbill species appeared to be more flexible in their occupancy of forest patches in this fragmented landscape. However, fruit resources, represented by hemi-epiphyte fig tree (*Ficus spp.*) density, were an important covariate in the occupancy models.

Large-bodied species are capable fliers (Tsuji et al. 1987, Poonsward and Tsuji 1994, Suryadi et al. 1998, Holbrook et al. 2002) and easily move between isolated forest patches in search of transient resources: in this case, widely dispersed fruit resources and nesting sites in large emergent trees with natural cavities. With this ability, larger species tend to be more frugivorous (Poonswad et al. 1983, Hadiprakarsa and Kinnaird 2004) and rely on patchily distributed fruit resources (Sitompul et al. 2004). As forest patch size decreases, the density of

resources may remain similar to larger forests, but the total number of resources declines.

Kinnaird and O'Brien (2007) suggested that the probability of finding a fruiting fig (*Ficus spp.*) at any given time, is much lower as forest size declines because of asynchronous fruiting.

Although fig density is an important predictor of the probability of a patch being occupied, we expect that fig density alone does not reflect availability of ripe fruit within the landscape.

Kannan and James (1999) suggested that fruit diversity within a fragmented landscape may be a more crucial aspect for hornbill communities (i.e., food is available all year round).

Kinnaird and O'Brien (2005) and Kinnaird et al. (1996) have demonstrated that hornbill density in large intact forests can be affected by the density of large strangling figs, and monthly variation in hornbill density is related to the availability of ripe fig fruit. It is possible that small patches do not contain enough large fig trees to ensure an adequate monthly food supply month to support resident populations. In such a situation, although a small patch might serve as a temporary source of food or nest-sites, self-sustaining populations would not be expected.

The availability of figs as a food source for the small-bodied territorial hornbills, *A. galeritus*, *B. comatus* and *A. corrugatus*, is of less importance to their occupancy. With movement restriction for this hornbill group, Leighton (1982) and Kinnaird and O'Brien (2007) suggested that these species tend to be more of a generalist in their diet preference and rely primarily on small fruit crops within a territory or have the ability to shift to alternate food sources such as animal prey, leaves or gum. Conversely, availability of potential nesting trees is more defensible for this group of species. This was explained when the potential nesting trees covariate the top ranked model in their occupancy model selection.

Most small hornbills are territorial and sedentary and are probably less inclined to venture to distant, unknown patches (Kinnaird and O'Brien 2007). Small-bodied territorial

hornbills were conspicuously absent from most forest patches, illustrating that small and isolated forest patches may not retain species with poor dispersal capabilities (Laidlaw 2000, Brook et al. 2003). Regardless of the size of forest patches within the fragmented landscape, small patches located within hornbill ranging distance of large patches is crucial to maintain a movement network to source patches, where vast hornbill resources are remain.

Management implications

The results from this study suggest that hornbills may be able to persist in fragmented landscapes. However, the ability to occupy forest patches was driven by species-specific requirements of resources, habitats and landscape configuration. Despite differences in number of species and occupancy, forests shared similar resource availability as well as levels of disturbance. This result supports the notion that small forests may simply not support enough trees to provide a sustaining resource base for a resident population of hornbills. In addition, degree of exchange among individuals within hornbill populations inhabit different forest patches has important implications for the maintenance of genetic diversity. We found that small-bodied territorial hornbills tend to be more affected by habitat fragmentation. When distance to the nearest vacant forest patch exceeds dispersal abilities, it is likely that the probability of occupy an isolated patch very low, and their populations may eventually disappear through a combination of stochastic events and habitat loss.

From a hornbill community perspective, the proximity of forest fragments and living in a large neighborhood comprised of a number of fragments within flying range is an essential key for their long-term persistence (Hadiprakarsa 2007; Kinnaird and O'Brien 2007). Therefore, in order to deploy effective hornbill conservation, the maintenance of remnant forest patches in

close proximity in a large neighborhood forest complex is required for long-term persistence of a Sumatran hornbill community.

LITERATURE CITED

- Anggraini, K., M. F. Kinnaird, and T. G. O'Brien. 2001. The effects of fruit availability and habitat disturbance on an assemblage of Sumatran hornbills. *Bird Conservation International* 10:189-202.
- Blake, J. G., and B. A. Loiselle. 1991. Variation in Resource Abundance Affects Capture Rates of Birds in Three Lowland Habitats in Costa Rica. *The Auk* 108:114-130.
- Brook, B. W., N. S. Sodhi, and P. K. L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* 424:420-426.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, K. Burnham, and L. Thomas. 2001. *Introduction to Distance Sampling: estimating abundance of biological populations*. Oxford University Press, Oxford.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference*. . Second Edition edition. Springer-Verlag, New York, USA.
- Cahill, A. J. 2003. Nest-site characteristics of the Red-knobbed Hornbill *Aceros cassidix* and Sulawesi Dwarf Hornbill *Penelopides exarhatus*. *Ibis* 145:E97-E113.
- Castelletta, M., N. S. Sodhi, and R. Subaraj. 2000. Heavy Extinctions of Forest Avifauna in Singapore: Lessons for Biodiversity Conservation in Southeast Asia. *Conservation Biology* 14:1870-1880.
- Christiansen, M. B., and E. Pitter. 1997. Species loss in a forest bird community near Lagoa Santa in southeastern Brazil. *Biological Conservation* 80:23-32.

- Datta, A. 1998. Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. *Oryx* 32:285-294.
- _____. 2001. An ecological study of sympatric hornbills and fruiting patterns in a tropical forest in Arunachal Pradesh. PhD Dissertation, Saurashtra University, Rajkot, India.
- Datta, A., and G. S. Rawat. 2003. Foraging Patterns of Sympatric Hornbills during the Nonbreeding Season in Arunachal Pradesh, Northeast India. *BIOTROPICA* 35:208-218.
- Donovan, T., and C. Flather. 2002. Relationships among north American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* 12:364-374.
- Foose, T. J., and N. van Strien. 1997. Asian Rhinos - Status survey and conservation action plan. IUCN, Gland, Switzerland and Cambridge, UK.
- Franklin, N., Bastoni, Sriyanto, D. Siswomartono, J. Manansang, and R. Tilson. 1999. Last of the Indonesian tigers: a causes for optimism. Pages 130-147 *in* J. Seidensticker, S. Christie, and P. Jackson, editors. *Riding the tiger: Tiger Conservation in Human-dominated Landscapes*. Cambridge University Press, Cambridge, UK.
- FWI/GFW. 2002. The State of the Forest: Indonesia. Forest Watch Indonesia, Bogor, Indonesia and Global Forest Watch, Washington, DC.
- Galleti, M. 1996. Fruits and frugivores in a Brazilian Atlantic Forest. PhD Dissertation, University of Cambridge, U. K.
- Gaveau, D. L. A., H. Wandono, and F. Setiabudi. 2007. Three decades of deforestation in southwest Sumatra: Have protected areas halted forest loss and logging, and promoted re-growth? *Biological Conservation* 134:495-504.
- Gibson, L., B. Wilson, D. Cahill, and J. Hill. 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *Journal of Applied Ecology* 41:213-223.

- Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife habitat models. *Biological Conservation* 116:195-203.
- Hadiprakarsa, Y., and M. F. Kinnaird. 2004. Foraging characteristics of an assemblage of four Sumatran hornbill species. *Bird Conservation International* 14:S53-S62.
- Hadiprakarsa, Y., M. F. Kinnaird, M. Iqbal, and T. G. O'Brien. 2007. Effects of forest fragmentation on hornbills across the southern Sumatran landscape. Pages 80-91 *in* Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4th International Hornbill Conference. Mabula Game Lodge, Bela-Bela, South Africa.
- Hedges, S., M. J. Tyson, A. F. Sitompul, M. F. Kinnaird, and D. Gunaryadi. 2005. Distribution, status, and conservation needs of Asian elephants (*Elephas maximus*) in Lampung Province, Sumatra, Indonesia. *Biological Conservation* 124:35-48.
- Holbrook, K. M., and T. B. Smith. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* 125:249-257.
- Holbrook, K. M., T. B. Smith, and B. D. Hardesty. 2002. Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* 25:745-749.
- Holmes, D. A. 2001. Deforestation in Indonesia: A Review of the Situation in Sumatra, Kalimantan, and Sulawesi. World Bank. Jakarta, Indonesia.
- Jenness, J. 2004. Nearest features (nearfeat. avx) extension for ArcView 3. x, v. 3.8a Available at, http://www.jennessent.com/arcview/nearest_features.htm.

- Kannan, R., and D. A. James. 1999. Fruiting Phenology and the Conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of Southern India. *BIOTROPICA* 31:167-177.
- Kanwatanakid-Savini, C., and P. Poonswad. 2007. Feeding ecology and food selection of four sympatric hornbill species at Khao Yai National Park, Thailand. Pages 195 in *Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4th International Hornbill Conference*. Mabula Game Lodge, Bela-Bela, South Africa.
- Kemp, A. 2001. Family Bucerotidae (hornbills). in J. del Hoyo, A. Elliot, and J. Sargatal, editors. *Handbook of the Birds of the World* Lynx Editions, Barcelona.
- Kinnaird, M., and T. G. O'Brien. 2007. *The Ecology and Conservation of Asian Hornbills: Farmers of the Forest*. The University of Chicago Press, Chicago.
- Kinnaird, M. F. 1998. Evidence for Effective Seed Dispersal by the Sulawesi Red-Knobbed Hornbill, *Aceros cassidix*. *BIOTROPICA* 30:50-55.
- Kinnaird, M. F., and T. G. O'Brien. 1999. Breeding ecology of the Sulawesi Red-Knobbed Hornbill *Aceros cassidix*. *Ibis* 141:60-69.
- _____. 2005. Fast Foods of The Forest: The Influence of Figs on Primates and Hornbills Across Wallace's Line. Pages 155-184 in J. L. Dew, and J. P. Boubli, editors. *Tropical Fruits and Frugivores: The Search for Strong Interactors*. Springer.
- Kinnaird, M. F., T. G. O'Brien, and S. Suryadi. 1996. Population fluctuation in Sulawesi Red-knobbed Hornbills: tracking figs in space and time. *Auk* 113:431-440.

- Kinnaird, M. F., E. W. Sanderson, T. G. O'Brien, H. T. Wibisono, and G. Woolmer. 2003. Deforestation Trends in a Tropical Landscape and Implications for Endangered Large Mammals. *Conservation Biology* 17:245-257.
- Laidlaw, R. K. 2000. Effects of Habitat Disturbance and Protected Areas on Mammals of Peninsular Malaysia. *Conservation Biology* 14:1639-1648.
- Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic Responses by Birds to Forest Fragmentation. *Conservation Biology* 19:1537-1546.
- Laurance, W. F. 1999. Reflections on the tropical deforestation crisis. *Biological Conservation* 91:109-117.
- Laurance, W. F., and R. O. Bierregaard. 1997. *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago.
- Lee, M., L. Fahrig, K. Freemark, and D. Currie. 2002. Importance of patch scale vs landscape scale on selected forest birds. *Oikos* 96:110-118.
- Leighton, M. 1982. *Fruit Resources and Patterns of Feeding, Spacing and Grouping Among Sympatric Bornean Hornbills (Bucerotidae)*. PhD Dissertation, University of California, Davis.
- Linkie, M., R. J. Smith, and N. Leader-Williams. 2004. Mapping and predicting deforestation patterns in the lowlands of Sumatra. *Biodiversity and Conservation* 13:1809-1818.
- MacKenzie, D. I. 2006. Modeling the Probability of Resource Use: The Effect of, and Dealing with, Detecting a Species Imperfectly. *Journal of Wildlife Management* 70:367-374.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines, editors. 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, San Diego, USA.

- MacKinnon, J., K. Phillipps, P. Andrew, and F. Rozendaal. 1993. A field guide to the birds of Borneo, Sumatra, Java, and Bali. Oxford University Press, Oxford.
- McGarigal, K., and W. C. McComb. 1995. Relationships Between Landscape Structure and Breeding Birds in the Oregon Coast Range. *Ecological Monographs* 65:235-260.
- Moore, J. E., and R. K. Swihart. 2005. Modeling patch occupancy by forest rodents: Incorporating detectability and spatial autocorrelation with hierarchically structured data. *Journal of Wildlife Management* 69:933-949.
- Newmark, W. D. 1991. Tropical fragmentation and the extinction of understorey birds in the Eastern Usambara mountains. *Conservation Biology* 5:67-78.
- O'Brien, T. G., M. F. Kinnaird, P. Jepson, and I. Setiawan. 1998. Effect of forest size and structure on the distribution of Sumba Wreathed Hornbills *Aceros everetti*. Pages 209-217 in *Proceedings of The Asian Hornbills: Ecology and Conservation, Proceedings of the Second Asian Hornbill Workshop, Bangkok*.
- Poonswad, P., V. Chimchome, K. Plongmai, and P. Chuailua. 2000. Factors influencing the reproduction of Asian Hornbills. Pages 1740-1755 in *Proceedings of the 22nd International Ornithological Congress, Durban*.
- Poonswad, P., a. Tsuji, and N. Jirawatkavi. 2004. Estimation of nutrients delivered to nest inmates by four sympatric species of hornbills in Khao Yai National Park, Thailand. *ORNITHOLOGICAL SCIENCE* 3:99-112.
- Poonswad, P., A. Tsuji, and C. Ngarmongsai. 1983. A study of the breeding biology of hornbills (Bucerotidae) in Thailand. Pages 239-265 in *Proceedings of a Delacour/International Foundation for the Conservation of Birds in Captivity*.

- _____. 1988. A comparative ecological study of four sympatric hornbills (Family Bucerotidae) in Thailand. *Acta XIX congressus Internationalis Ornithologi* 2:2781-2791.
- Poonsward, P., and A. Tsuji. 1994. Ranges of males of the great hornbill *Buceros bicornis*, brown hornbill *Ptilolaemus tickelli* and wreathed hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis* 136:79-86.
- Rabus, B., M. Einder, A. Roth, and R. Balmer. 2003. The shuttle rada topography mission-a new class of digital elevation models acquired by spaceborne radar. *Photogrammetry and Remote Sensing* 57:241-262.
- Radford, J. Q., and A. F. Bennett. 2007. The relative importance of landscape properties for woodland birds in agricultural environments. *Journal of Applied Ecology* 44:737-747.
- Raman, T., and D. Mudappa. 2003. Correlates of hornbill distribution and abundance in rainforest fragments in the southern Western Ghats, India. *Bird Conservation International* 13:199-212.
- Rampel, R. S., and A. Carr. 2003. Patch analyst Extension for ArcView 2.3. Available at, <http://flash.lakeheadu.ca/~rrempe/patch/index.html>.
- Sanderson, E. W., K. H. Redford, A. Vedder, P. B. Coppolillo, and S. E. Ward. 2002. A conceptual model for conservation planning based on landscape species requirements. *Landscape and Urban Planning* 58:41-56.
- Sieving, K. E., and J. R. Karr. 1997. Avian extinction and persistence mechanisms in lowland Panama. Pages 156-170 *in* W. F. Laurance, and R. O. Bierregaard, editors. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. . University of Chicago Press, Chicago.

- Sitompul, A. F., M. F. Kinnaird, and T. G. O'Brien. 2004. Size matters: the effects of forest fragmentation and resource availability on the endemic Sumba Hornbill *Aceros everetti*. *Bird Conservation International* 14:S23-S37.
- Sodhi, N. S., T. M. Lee, L. P. Koh, and R. R. Dunn. 2005. A century of avifaunal turnover in a small tropical rainforest fragment. *Animal Conservation* 8:217-222.
- Stouffer, P. C., and R. O. Bierregaard. 1995. Use of Amazonian Forest Fragments by Understory Insectivorous Birds. *Ecology* 76:2429-2445.
- Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy. 2006. Long-Term Landscape Change and Bird Abundance in Amazonian Rainforest Fragments. *Conservation Biology* 20:1212-1223.
- Suryadi, S., M. F. Kinnaird, and T. G. O'Brien. 1998. Home ranges and daily movements of the Sulawesi red-knobbed hornbill *Aceros cassidix* during the non-breeding season. Pages 159-170 *in* Proceedings of The Asian hornbills: ecology and conservation. Thai Studies in Biodiversity.
- Telleria, J. L., R. Baquero, and T. Santos. 2003. Effects of forest fragmentation on European birds: implications of regional differences in species richness. *Journal of Biogeography* 30:621-628.
- Tsuji, A., P. Poonswad, and N. Jirawatkari. 1987. Application of radio tracking to study ranging pattern of hornbills (Bucerotidae) in Thailand. Pages 316-351 *in* Proceedings of Proceedings of the Jean Delacour/International Foundation for the Conservation of Birds Symposium on Breeding Birds in Captivity.

- van Marle, J. G., and K. H. Voous. 1988. The birds of Sumatra: an annotated check-list. Pages 1-265 *in* British Ornithological Union Check-list 10. British Ornithological Union, Tring, UK.
- Veech, J. A. 2006. Increasing and Declining Populations of Northern Bobwhites Inhabit Different Types of Landscapes. *Journal of Wildlife Management* 70:922-930.
- Villard, M.-A., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation Effects on Forest Birds: Relative Influence of Woodland Cover and Configuration on Landscape Occupancy. *Conservation Biology* 13:774-783.
- Waltert, M., A. Mardiasuti, and M. Muhlenberg. 2004. Effects of Land Use on Bird Species Richness in Sulawesi, Indonesia. *Conservation Biology* 18:1339-1346.
- Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology & Evolution* 17:379-385.
- Watson, J. E. M., R. J. Whittaker, and T. P. Dawson. 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. Pages 311-327 *in*.
- Wiens, J., J. Rotenberry, and B. Horne. 1987. Habitat Occupancy Patterns of North American Shrubsteppe Birds: The Effects of Spatial Scale. *Oikos* 48:132-147.
- Wiens, J. A. 1992. The ecology of bird communities. Volume 1. Foundations and patterns. Cambridge University Press, New York.
- World Bank. 2001. Indonesia: Environment and Natural Resource Management in a Time of Transition. The World Bank. Washington D.C.

Table 2.1. Scientific names with weight, territorial, elevation distributions, and home range and daily travels for nine species of Sumatran hornbill.

| Species ^a | Weight (g) ^b | Territorial ^{b,c} | Elevation distribution (m) ^{b,g} | Home range (km ²) | Daily travel (km) |
|----------------------|-------------------------|----------------------------|---|-------------------------------|----------------------|
| <i>Rhyticeros</i> | | | | | |
| <i>undulatus</i> | 1,950 - 2,515 | no | 0 - 2500 | 28 ^d | 10 - 15 ^d |
| <i>corrugatus</i> | 1,273 - 1,590 | no | 0 - 200 | ? | |
| <i>Buceros</i> | | | | | |
| <i>rhinoceros</i> | 2,180 - 2,580 | no | 0 - 1000 | ? | > 3 ^{c,h} |
| <i>bicornis</i> | 2,211 - 3,400 | no | 0 - 1000 | 16.9 ^d | 10 - 15 ^d |
| <i>Rhinoplax</i> | | | | | |
| <i>vigil</i> | 2,500 - 3,100 | no | 0 - 1000 | ? | |
| <i>Berenicornis</i> | | | | | |
| <i>comatus</i> | 1,470 - 1,476 | yes | 0 - 1000 | ? | < 2 ^{c,h} |
| <i>Anorrhinus</i> | | | | | |
| <i>galerritus</i> | 933 - 1,172 | yes | 0 - 1800 | 1.5 ^f | < 2.5 ^{c,h} |
| <i>Anthracoceros</i> | | | | | |
| <i>albirostris</i> | 624 - 738 | yes | 0 - 700 | 5 ^e | 4 |
| <i>malayanus</i> | 633 - 1,050 | yes | 0 - 200 | 3.3 | 2 ^{c,h} |

^a Kemp 2001; ^b Kemp 1995; ^c Kinnaird and O'Brien 2007; ^d Poonswad and Tsuji 1994; ^e Tsuji et al. 1986; ^f WCS-IP Unpublished data;

^g MacKinnon et al. 1993; ^h Simulation result

Table 2.2. Patch and transect characteristics in sampled areas, Lampung Province, Sumatra, Indonesia.

| No | Forest Patch | Protection Status* | Category± | Transect Length (Km) | Number of Transect | Replication |
|----|-------------------------------|--------------------|-----------|----------------------|--------------------|-------------|
| 1 | Bukit Barisan Selatan (North) | NP | O | 4 | 2 | 4 |
| 2 | Bukit Barisan Selatan (South) | NP | O | 22.2 | 11 | 44 |
| 3 | G. Tanggang | NR | S, I | 2 | 1 | 4 |
| 4 | G. Seminung | NR | S | 2 | 1 | 4 |
| 5 | Air Nanningan Kecil | NR | S, I | 2 | 1 | 4 |
| 6 | Mulang Mayang | LF | S | 2 | 2 | 4 |
| 7 | G. Betung | NR | S, I | 2 | 1 | 4 |
| 8 | Lima Kunci | NP | S | 2 | 1 | 4 |
| 9 | G. Pesawaran | NR | M, I | 3 | 2 | 4 |
| 10 | G. Pesagi | NR | M, | 4 | 2 | 4 |
| 11 | G. Rajabasa | NR | M, I | 3 | 2 | 4 |
| 12 | G. Tanggamus | NR | M, I | 2.7 | 2 | 4 |
| 13 | G. Sekincau | NP | M | 2.4 | 2 | 6 |
| 14 | Batu Tegi | NR | L | 5.74 | 2 | 4 |
| 15 | Tangkit Tebak | NR | L, I | 4.2 | 3 | 4 |
| 16 | Ulu Belu | NR | L | 3 | 2 | 8 |
| 17 | Way Kambas | NP | L, I | 25 | 15 | 17 |
| 18 | Lombok Area | NP | L | 6 | 3 | 6 |

*NP = National Park; NR = Nature Reserve; LF = Limited production forest ±O = Source area; S = Small; M = Medium; L = Large; I = Isolated.

Table 2.3. Description of covariates used in occupancy estimation as a function of resource selection and habitat relationships in Lampung Province, Sumatra, Indonesia.

| No | Covariate | Code | Variable Type | Data type | Values |
|-----------|--------------------------------|-------------|----------------------|------------------|--------------------------------|
| 1 | Human disturbance | Dist | Habitat quality | Categorical | 1 = High, 0 = Low |
| 2 | Potential nesting tree density | Pods | Resources | Continuous | 0 - 10.7 trees/ha |
| 3 | Figs density | Figs | Resources | Continuous | 0 - 4.96 trees/ha |
| 4 | Patch size | Size | Landscape | Continuous | 159.89 - 149,505 ha |
| 5 | Patch isolation | Isol | Landscape | Continuous | 1 = Isolated, 0 = Not isolated |
| 6 | Elevation | Elev | Landscape | Continuous | 22.8 - 1,806.54 m |
| 7 | Slope | Slop | Landscape | Continuous | 0.71 - 37.56 degree |

Table 2.4. Estimates of occupancy (ψ) and detection probability (p) from the top ranked models for seven hornbill species as a function of resource selection in Lampung Province, Sumatra, Indonesia.

| | Model | ΔAIC | w | K | -2l | $\hat{\psi}$ | s.e | \hat{p} | Naïve |
|-------------------------|--|-------------------------------|----------|----------|------------|--------------------------------|---------------|-----------------------------|--------------|
| <i>1. B. rhinoceros</i> | | | | | | | | | |
| 1.1 | ψ (Figs + Pods), p (Elev + Size + Isol) | 0.00 | 0.36 | 7 | 244.15 | 0.681 | 0.115 | 0.531 | 0.6071 |
| 1.2 | ψ (Figs), p (Elev + Size + Isol) | 0.70 | 0.25 | 6 | 246.85 | 0.716 | 0.093 | 0.519 | |
| 1.3 | ψ (Pods), p (Elev + Size + Isol) | 0.98 | 0.22 | 6 | 247.13 | 0.685 | 0.102 | 0.531 | |
| 1.4 | ψ (.), p (Elev + Size + Isol) | 1.57 | 0.16 | 5 | 249.72 | 0.725 | 0.074 | 0.516 | |
| 1.5 | ψ (Figs + Pods), p (Size) | 5.09 | 0.03 | 5 | 253.24 | 0.641 | 0.108 | 0.600 | |
| | Model averaged | | | | | 0.716 | 0.125 | | |
| <i>2. B. bicornis</i> | | | | | | | | | |
| 2.1 | ψ (Figs), p (.) | 0.00 | 0.38 | 3 | 47.66 | 0.758 | 0.497 | 0.030 | 0.0893 |
| 2.2 | ψ (Figs), p (Elev) | 1.52 | 0.18 | 4 | 47.18 | 0.729 | 0.480 | 0.033 | |
| 2.3 | ψ (Figs), p (Isol) | 1.55 | 0.18 | 4 | 47.21 | 0.760 | 0.513 | 0.031 | |
| 2.4 | ψ (Figs), p (Size) | 1.98 | 0.14 | 4 | 47.64 | 0.742 | 0.485 | 0.031 | |
| 2.5 | ψ (Figs), p (Elev + Size + Isol) | 5.16 | 0.03 | 6 | 46.82 | 0.744 | 0.551 | 0.034 | |
| | Model averaged | | | | | 0.682 | 0.1621 | | |

Notes: ψ is the probability a site is occupied by hornbill species and p is the probability of detecting hornbill in j th survey where $\psi(\cdot)$ $p(\cdot)$ assumes that hornbills presence and detection probability are constant across sites, Δ AIC is the difference in AIC values between each model with the low (best) model, w is the AIC model weight, K is the number of parameters in the model, $-2l$ is twice the negative log-likelihood e , $\hat{\psi}$ is the estimated overall occupancy probability, \hat{p} is the estimated overall detection probability.

(Continued)

Table. 2.4. Continued

| | Model | Δ AIC | w | K | -2l | $\hat{\psi}$ | s.e | \hat{p} | Naïve |
|------------------------|--|--------------|------|----------|------------|--------------|--------------|-----------|--------------|
| <i>3. R. vigil</i> | | | | | | | | | |
| 3.1 | ψ (Figs + Pods), p (Elev + Size + Isol) | 0.00 | 0.28 | 7 | 143.94 | 0.480 | 0.148 | 0.269 | 0.286 |
| 3.2 | ψ (Pods), p (Elev + Size + Isol) | 0.58 | 0.21 | 6 | 146.52 | 0.494 | 0.147 | 0.263 | |
| 3.3 | ψ (Figs + Pods), p (Size) | 1.03 | 0.17 | 5 | 148.97 | 0.415 | 0.116 | 0.404 | |
| 3.4 | ψ (.), p (Elev + Size + Isol) | 1.35 | 0.14 | 5 | 149.29 | 0.578 | 0.125 | 0.246 | |
| 3.5 | ψ (Figs), p (Elev + Size + Isol) | 2.07 | 0.10 | 6 | 148.01 | 0.571 | 0.144 | 0.249 | |
| 3.6 | ψ (Pods), p (Size) | 2.26 | 0.09 | 4 | 152.20 | 0.400 | 0.103 | 0.405 | |
| | Model averaged | | | | | 0.488 | 0.200 | | |
| <i>4. R. undulatus</i> | | | | | | | | | |
| 4.1 | ψ (.), p (.) | 0.00 | 0.16 | 2 | 193.59 | 0.661 | 0.126 | 0.249 | 0.466 |
| 4.2 | ψ (.), p (Size) | 0.14 | 0.15 | 3 | 191.73 | 0.632 | 0.115 | 0.271 | |
| 4.3 | ψ (Figs), p (.) | 0.61 | 0.12 | 3 | 192.20 | 0.652 | 0.149 | 0.252 | |
| 4.4 | ψ (Pods), p (.) | 0.87 | 0.11 | 3 | 192.46 | 0.673 | 0.152 | 0.247 | |
| 4.5 | ψ (.), p (Elev) | 0.97 | 0.10 | 3 | 192.56 | 0.653 | 0.125 | 0.260 | |
| 4.6 | ψ (Pods), p (Size) | 1.35 | 0.08 | 4 | 190.94 | 0.643 | 0.144 | 0.265 | |
| 4.7 | ψ (Figs), p (Size) | 1.55 | 0.08 | 4 | 191.14 | 0.621 | 0.144 | 0.271 | |
| 4.8 | ψ (Figs + Pods), p (.) | 1.61 | 0.07 | 4 | 191.20 | 0.663 | 0.167 | 0.250 | |
| 4.9 | ψ (.), p (Isol) | 1.96 | 0.06 | 3 | 193.55 | 0.666 | 0.133 | 0.248 | |
| 4.10 | ψ (Figs), p (Elev) | 1.97 | 0.06 | 4 | 191.56 | 0.642 | 0.152 | 0.262 | |
| 4.12 | ψ (Pods), p (Elev) | 2.21 | 0.05 | 4 | 191.80 | 0.663 | 0.153 | 0.255 | |
| | Model averaged | | | | | 0.682 | 0.162 | | |

(Continued)

Table. 2.4. Continued

| | Model | ΔAIC | w | K | -2l | $\hat{\psi}$ | s.e | \hat{p} | Naïve |
|-------------------------|-----------------------------|--------------------|------|----------|------------|--------------|--------------|-----------|--------------|
| <i>5. A. corrugatus</i> | | | | | | | | | |
| 5.1 | ψ (.), p (.) | 0.00 | 0.72 | 2 | 46.47 | 0.091 | 0.049 | 0.337 | 0.0714 |
| 5.2 | ψ (Figs), p (.) | 1.91 | 0.28 | 3 | 46.38 | 0.091 | 0.062 | 0.338 | |
| | Model averaged | | | | | 0.091 | 0.003 | | |
| <i>6. B. comatus</i> | | | | | | | | | |
| 6.1 | ψ (.), p (Isol) | 0.00 | 0.24 | 3 | 26.71 | 0.216 | 0.196 | 0.044 | 0.0357 |
| 6.2 | ψ (.), p (.) | 0.64 | 0.18 | 2 | 29.35 | 0.119 | 0.126 | 0.090 | |
| 6.3 | ψ (Pods), p (Isol) | 1.57 | 0.11 | 4 | 26.28 | 0.271 | 0.353 | 0.041 | |
| 6.4 | ψ (.), p (Elev) | 1.69 | 0.11 | 3 | 28.40 | 0.121 | 0.119 | 0.087 | |
| 6.5 | ψ (Figs), p (Elev) | 1.84 | 0.10 | 4 | 26.55 | 0.124 | 0.148 | 0.087 | |
| 6.6 | ψ (Pods), p (.) | 2.53 | 0.07 | 3 | 29.24 | 0.124 | 0.154 | 0.089 | |
| 6.7 | ψ (.), p (Size) | 2.64 | 0.07 | 3 | 29.35 | 0.118 | 0.135 | 0.090 | |
| 6.8 | ψ (Figs + Pods), p (.) | 2.91 | 0.06 | 4 | 27.62 | 0.126 | 0.186 | 0.086 | |
| 6.9 | ψ (Pods), p (Elev) | 3.26 | 0.05 | 4 | 27.97 | 0.148 | 0.184 | 0.087 | |
| 6.10 | ψ (Pods), p (Size) | 4.53 | 0.03 | 4 | 29.24 | 0.120 | 0.157 | 0.092 | |
| | Model averaged | | | | | 0.162 | 0.072 | | |

(Continued)

Table. 2.4. Continued

| Model | | ΔAIC | w | K | $-2l$ | $\hat{\psi}$ | $s.e$ | \hat{p} | |
|------------------------|--------------------------------|--------------------|------|-----|--------|--------------|--------------|-----------|--------|
| <i>7. A. galeritus</i> | | | | | | | | | |
| 7.1 | ψ (Pods), p (Isol) | 0.00 | 0.17 | 4 | 173.43 | 0.581 | 0.156 | 0.258 | 0.3750 |
| 7.2 | ψ (Pods), p (Elev) | 0.18 | 0.16 | 4 | 173.61 | 0.680 | 0.188 | 0.212 | |
| 7.3 | ψ (Pods), p (.) | 0.23 | 0.16 | 3 | 175.66 | 0.647 | 0.161 | 0.218 | |
| 7.4 | ψ (Figs + Pods), p (Isol) | 1.42 | 0.09 | 5 | 172.85 | 0.553 | 0.165 | 0.272 | |
| 7.5 | ψ (.), p (Elev) | 1.51 | 0.08 | 3 | 176.94 | 0.686 | 0.164 | 0.213 | |
| 7.6 | ψ (Pods), p (Size) | 1.73 | 0.07 | 4 | 175.16 | 0.679 | 0.180 | 0.206 | |
| 7.7 | ψ (Figs + Pods), p (Elev) | 2.00 | 0.06 | 5 | 173.43 | 0.643 | 0.201 | 0.222 | |
| 7.8 | ψ (Figs + Pods), p (.) | 2.02 | 0.06 | 4 | 175.45 | 0.621 | 0.178 | 0.226 | |
| 7.9 | ψ (.), p (Isol) | 2.10 | 0.06 | 3 | 177.53 | 0.555 | 0.123 | 0.272 | |
| 7.10 | ψ (Figs), p (Elev) | 2.81 | 0.04 | 4 | 176.24 | 0.684 | 0.187 | 0.214 | |
| Model averaged | | | | | | 0.612 | 0.176 | | |

Table 2.5. Estimates (ψ) and detection probability (p) from the top ranked models for seven hornbill species as a function of habitat relationships in Lampung Province, Sumatra, Indonesia.

| | Model | AIC | ΔAIC | w | K | -2l |
|-------------------------|--|------------|-------------------------------|----------|----------|------------|
| <i>1. B. rhinoceros</i> | | | | | | |
| 1.1 | psi(Elev + Dist),p(Elev) | 251.9 | 0.00 | 1.00 | 5 | 241.90 |
| 1.2 | psi(Isol + Dist),p(Elev) | 264.8 | 12.88 | 0.00 | 5 | 254.78 |
| 1.3 | psi(Elev + Size + Isol + Dist),p(Elev) | 269 | 17.10 | 0.00 | 7 | 255.00 |
| <i>2. B. bicornis</i> | | | | | | |
| 2.1 | psi(Dist),p(.) | 53.15 | 0.00 | 0.26 | 3 | 47.15 |
| 2.2 | psi(Isol),p(.) | 53.47 | 0.32 | 0.22 | 3 | 47.47 |
| 2.3 | psi(Dist),p(Elev) | 53.75 | 0.60 | 0.19 | 4 | 45.75 |
| 2.4 | psi(Dist),p(Isol) | 54.64 | 1.49 | 0.12 | 4 | 46.64 |
| 2.5 | psi(Dist),p(Size) | 55.08 | 1.93 | 0.10 | 4 | 47.08 |
| 2.6 | psi(Isol),p(Elev) | 55.19 | 2.04 | 0.09 | 4 | 47.19 |
| <i>3. R. vigil</i> | | | | | | |
| 3.1 | psi(Elev),p(Size) | 158.2 | 0.00 | 0.66 | 4 | 150.17 |
| 3.2 | psi(Elev + Dist),p(Size) | 159.8 | 1.65 | 0.29 | 5 | 149.82 |
| 3.3 | psi(Elev + Size + Isol),p(.) | 164.3 | 6.17 | 0.03 | 5 | 154.34 |
| 3.4 | psi(Elev + Size + Isol),p(Elev) | 165.6 | 7.41 | 0.02 | 6 | 153.58 |
| 3.5 | psi(Elev + Size + Isol + Dist),p(.) | 166.2 | 8.01 | 0.01 | 6 | 154.18 |

Notes: ψ is the probability a site is occupied by hornbill species and p is the probability of detecting hornbill in j th survey, Δ AIC is the difference in AIC values between each model with the low model, w is the AIC model weight, K is the number of parameters in the model, $-2l$ is twice the negative log-likelihood.

(Continued)

Table 2.5. Continued

| | Model | AIC | Δ AIC | w | K | -2l |
|-------------------------|--------------------------|-------|--------------|------|---|--------|
| <i>4. R. undulatus</i> | | | | | | |
| 4.1 | psi(Size),p(Size) | 190.4 | 0.00 | 0.86 | 4 | 182.44 |
| 4.2 | psi(Size),p(Elev) | 194.6 | 4.18 | 0.11 | 4 | 186.62 |
| 4.3 | psi(Isol + Dist),p(Size) | 198 | 7.51 | 0.02 | 5 | 187.95 |
| 4.4 | psi(Isol + Dist),p(.) | 199.6 | 9.12 | 0.01 | 4 | 191.56 |
| 4.5 | psi(Isol + Dist),p(Elev) | 200 | 9.59 | 0.01 | 5 | 190.03 |
| <i>5. A. corrugatus</i> | | | | | | |
| 5.1 | psi(Isol),p(.) | 46.57 | 0.00 | 0.55 | 3 | 40.57 |
| 5.2 | psi(Dist),p(.) | 46.95 | 0.38 | 0.45 | 3 | 40.95 |
| <i>6. B. comatus</i> | | | | | | |
| 6.1 | psi(.),p(.) | 33.35 | 0.00 | 0.14 | 2 | 29.35 |
| 6.2 | psi(Dist),p(Elev) | 33.93 | 0.58 | 0.10 | 4 | 25.93 |
| 6.3 | psi(Size),p(Elev) | 34.04 | 0.69 | 0.10 | 4 | 26.04 |
| 6.4 | psi(Elev),p(Elev) | 34.37 | 1.02 | 0.08 | 4 | 26.37 |
| 6.5 | psi(.),p(Elev) | 34.4 | 1.05 | 0.08 | 3 | 28.40 |
| 6.6 | psi(Size),p(Isol) | 34.56 | 1.21 | 0.07 | 4 | 26.56 |
| 6.7 | psi(Dist),p(.) | 34.57 | 1.22 | 0.07 | 3 | 28.57 |
| 6.8 | psi(Isol),p(Isol) | 34.71 | 1.36 | 0.07 | 4 | 26.71 |
| 6.9 | psi(Size),p(.) | 34.86 | 1.51 | 0.06 | 3 | 28.86 |
| 6.10 | psi(Elev),p(.) | 35.02 | 1.67 | 0.06 | 3 | 29.02 |
| 6.11 | psi(.),p(Size) | 35.35 | 2 | 0.05 | 3 | 29.35 |

(Continued)

Table 2.5. Continued

| | Model | AIC | ΔAIC | w | K | -2l |
|------------------------|--------------------------|------------|-------------------------------|-----------------------|----------|------------|
| <i>7. A. galeritus</i> | | | | | | |
| 7.1 | psi(Isol + Dist),p(Isol) | 178.7 | 0.00 | 0.26 | 5 | 168.71 |
| 7.2 | psi(Elev),p(Isol) | 179.2 | 0.00 | 0.25 | 4 | 171.19 |
| 7.3 | psi(Elev),p(.) | 179.9 | 0.73 | 0.18 | 3 | 173.92 |
| 7.4 | psi(Elev),p(Elev) | 181.5 | 2.31 | 0.08 | 4 | 173.50 |
| 7.5 | psi(Size),p(Isol) | 181.5 | 2.32 | 0.08 | 4 | 173.51 |
| 7.6 | psi(Dist),p(Isol) | 181.7 | 2.53 | 0.07 | 4 | 173.72 |
| 7.7 | psi(Elev),p(Size) | 181.8 | 2.60 | 0.07 | 4 | 173.79 |
| 7.8 | psi(Dist),p(.) | 182.7 | 3.50 | 0.04 | 3 | 176.69 |
| 7.9 | psi(.),p(Elev) | 182.9 | 3.75 | 0.04 | 3 | 176.94 |
| 7.10 | psi(Dist),p(Elev) | 183.1 | 3.88 | 0.04 | 4 | 175.07 |
| 7.11 | psi(.),p(Isol) | 183.5 | 4.34 | 0.03 | 3 | 177.53 |
| 7.12 | psi(Size),p(.) | 183.7 | 4.55 | 0.03 | 3 | 177.74 |

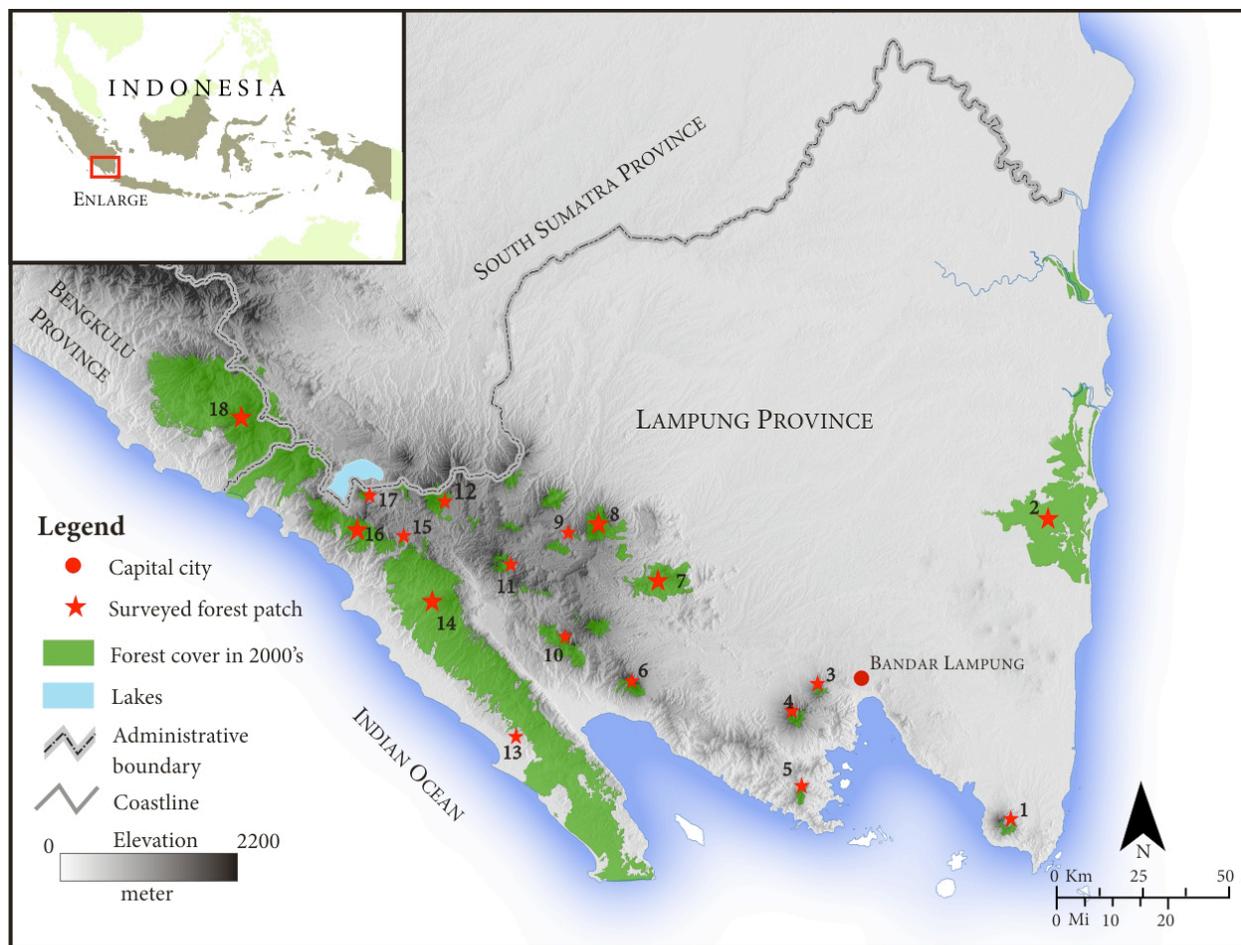


Figure 2.1. Map of study area in southern Sumatra landscape, Indonesia. Enlargement shows forest cover in 2000's, elevation and surveyed forest patch locations.

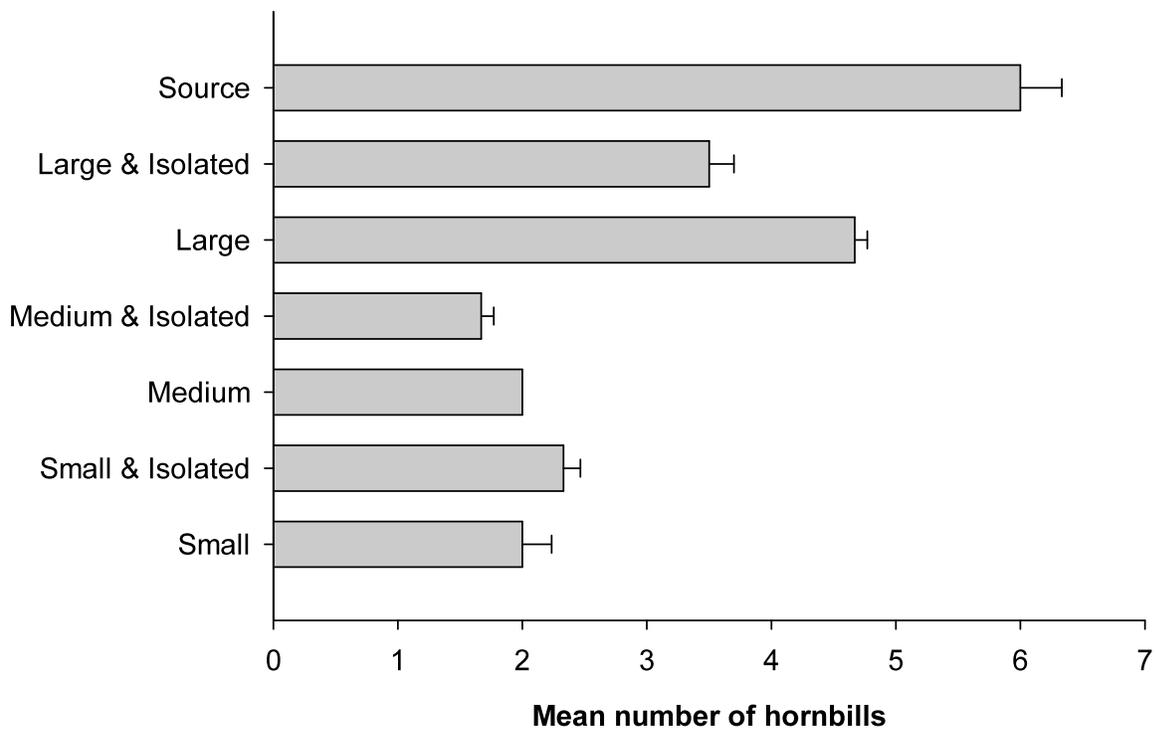


Figure 2.2. Distribution of nine hornbill species in forest patch categories by size and patch isolation in Lampung Province, Sumatra, Indonesia.

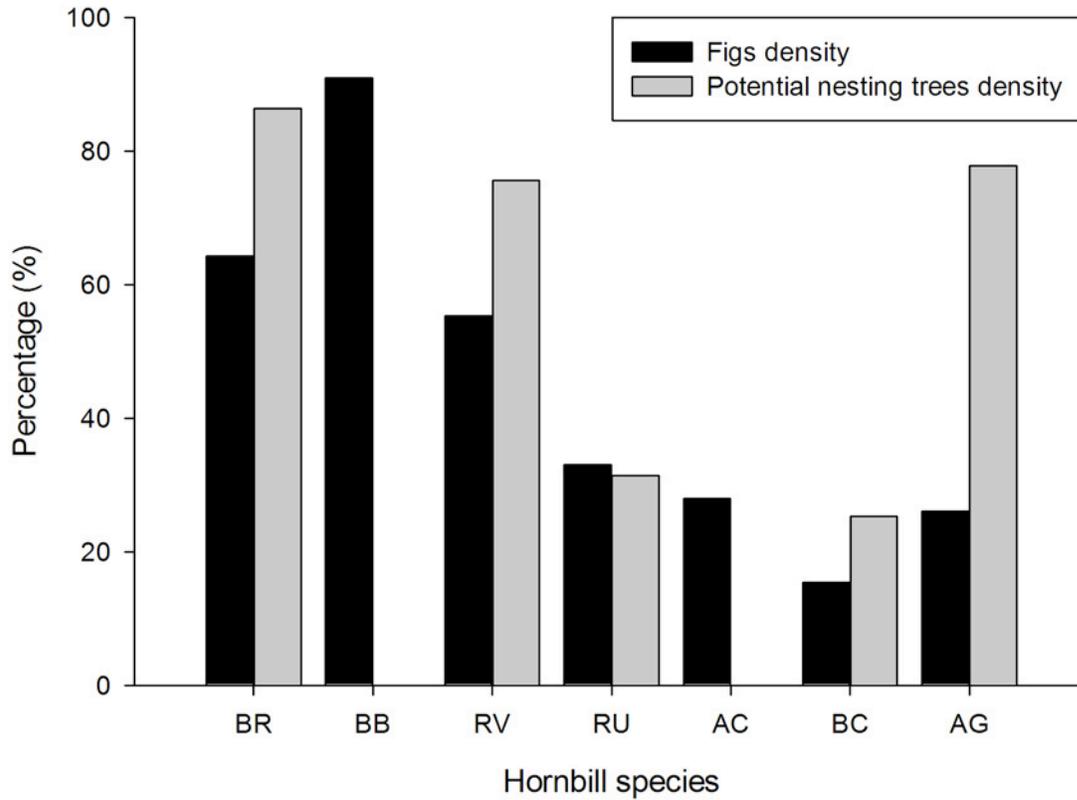


Figure 2.3. Total summed model of proportion of patch occupied as a function of resource selection for seven hornbill species in Lampung Province, Sumatra, Indonesia. (Abbreviations: BR = *B. rhinoceros*; BB = *B. bicornis*; RV = *R. vigil*; RU = *R. undulatus*; AC = *A. corrugatus*; BC = *B. comatus*; AG = *A. galeritus*).

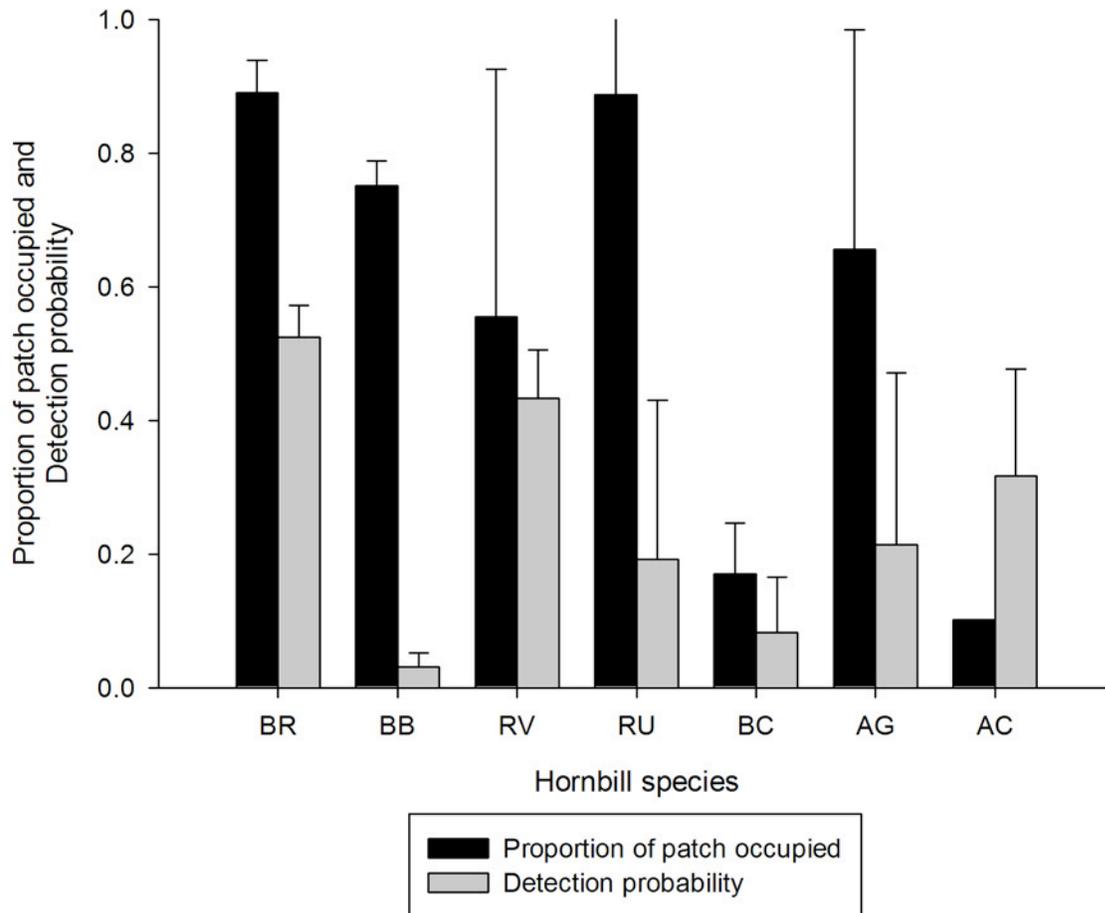


Figure 2.4. General parameter estimates from the best model for proportion of patch occupied and detection probability (mean + 1SE) as a function of habitat relationships for seven Sumatran hornbill species in Lampung Province, Sumatra, Indonesia. (Abbreviations: BR = *B. rhinoceros*; BB = *B. bicornis*; RV = *R. vigil*; RU = *R. undulatus*; AC = *A. corrugatus*; BC = *B. comatus*; AG = *A. galeritus*).

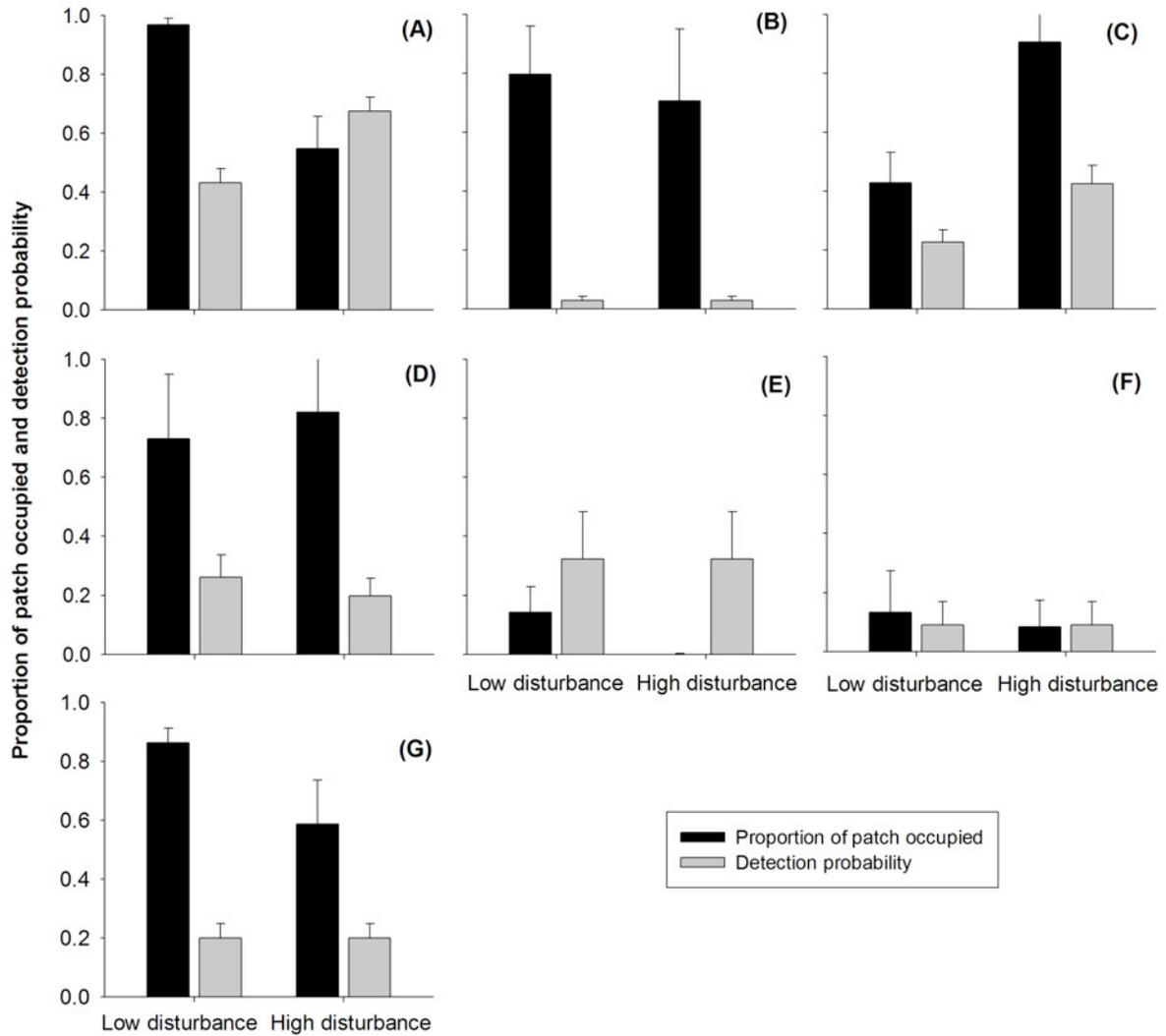


Figure 2.5. Parameter estimates with species-specific habitat disturbance covariates (mean + 1SE). Proportion of patch occupied and detection probability for seven Sumatran hornbill species in Lampung Province, Sumatra, Indonesia. (A) *B. rhinoceros*; (B) *B. bicornis*; (C) *R. vigil*; (D) *R. undulatus*; (E) *A. corrugatus*; (F) *B. comatus*; (G) *A. galeritus*.

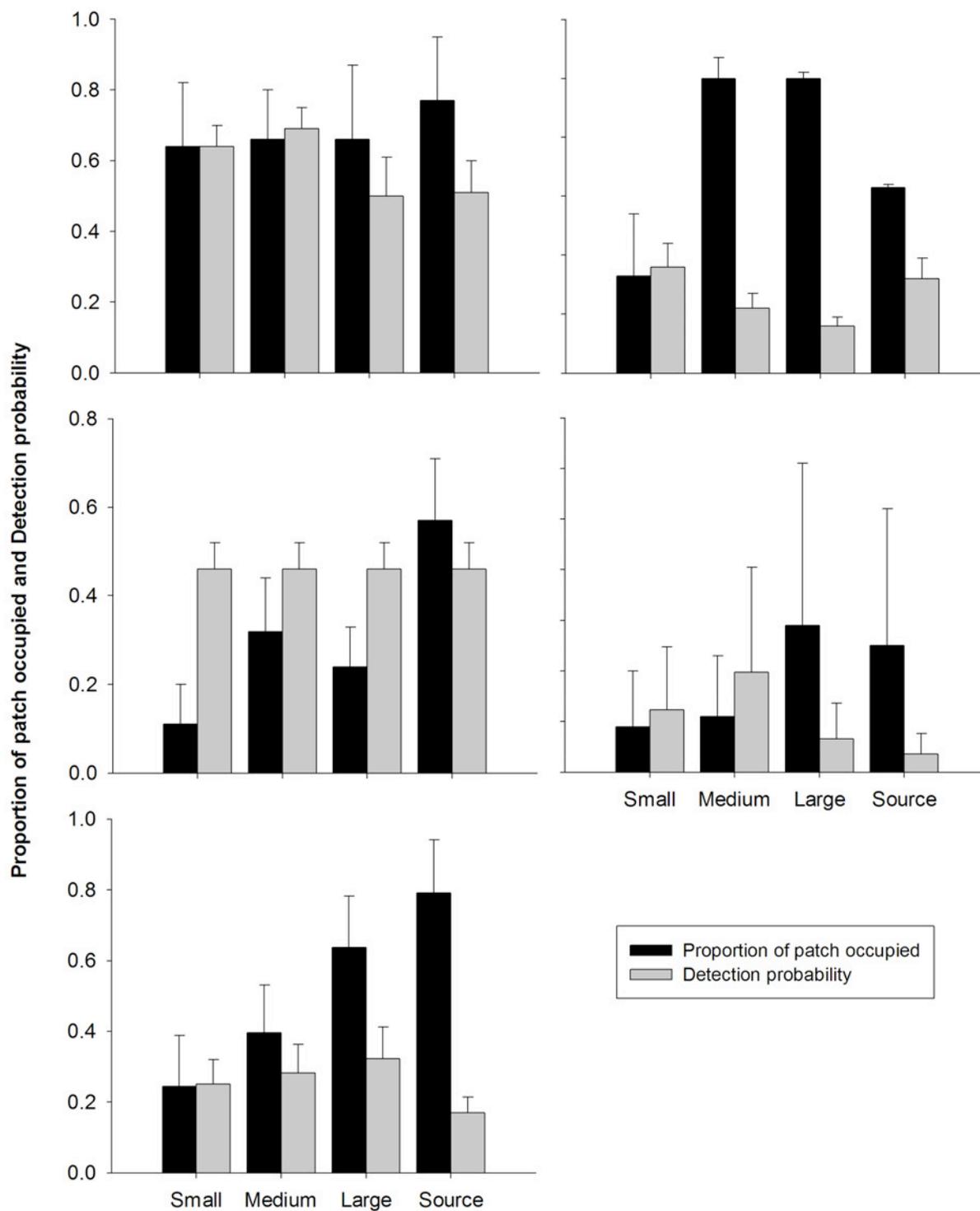


Figure 2.6. Parameter estimates with species-specific response to forest patch size covariates (mean + 1SE). Bars represent proportion of patch occupied and detection probability for five Sumatran hornbill species in Lampung Province, Sumatra, Indonesia. (A) *B. rhinoceros*; (B) *R. undulatus*; (C) *R. vigil*; (D) *B. comatus*; (E) *A. galeritus*.

CHAPTER 3

PREDICTING PROBABILITY OF OCCURRENCE OF SUMATRAN HORNBILLS IN A FRAGMENTED LANDSCAPE IN SOUTHERN SUMATRA, INDONESIA¹

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ABSTRACT

Management and conservation of wide ranging species is difficult due to their requirements of space and resources. Hornbills in Southeast Asia are large birds and are capable of utilizing large blocks of habitat on forested landscapes to satisfy their daily requirements. However, hornbill persistence has been threatened due to extensive deforestation and the trend has been for rapid decline in the future. We develop spatially explicit habitat models (SEHM), based on habitat, human impacts, and occupancy analysis on 18 forests and fragments, for four Sumatran hornbills (*Anorrhinus galeritus*, *Buceros rhinoceros*, *Rhinoplax vigil*, and *Ryhticeros undulatus*) to predict probability of their occurrence in a fragmented landscape in southern Sumatra, Indonesia.

Among the three large-bodied generalist species, elevation and slope were important parameters for species detection rate and occupancy. The importance of proximity to the settlements for detecting *A. galeritus* may be explained indirectly on the predictive model results. Although our models predicting occurrence were noisy, we found that to obtain robust predictive modeling results for hornbill occurrences at broad scale, we suggest to cautiously choosing modeling development strategy. To improve hornbill sampling design protocol, we suggest more evaluation of survey techniques to improve detection rates. Our modeling results showed great potential of this method to predicting hornbill occurrences that can be use as an alternative tool to land managers to develop conservation priorities for Sumatran hornbills.

INTRODUCTION

More than 50% of natural habitats have been destroyed in tropical countries of the world; much of this has been tropical rainforest (World Resources Institute 2000). Consequently, wildlife populations have been forced to persist in forest pockets across fragmented landscapes that are surrounded by a human-made matrix (Greenberg 1996, Bunnell 1999). The management

and conservation of wide ranging species is especially difficult due to their large requirements of space (Mortberg 2001, Osborne et al. 2001, Schadt et al. 2002, Kinnaird and O'Brien 2007).

Conservation plans require an extensive knowledge of the species and how they utilize various components of their ecosystems (Sanderson et al. 2002, Schadt et al. 2002, Shriner et al. 2006). However, gathering this information requires a significant resource and often this information is unavailable or is derived only from a single site.

With an alarming rate of forest loss, of the formerly forested landscape of Indonesia has deteriorated and become fragmented by anthropogenic activity (Kinnaird and O'Brien 2007). During the last 20 years, the island of Sumatra has experienced some of the highest rates of deforestation in the world (e.g. Laurance 1999, Holmes 2001). During 1985 – 1997, 6.7 million ha of forest were lost (FWI/GFW 2002) and all major protected areas on the island were impacted (Kinnaird et al. 2003, Linkie et al. 2004, Gaveau et al. 2007). Lampung Province, the southernmost province on the island, has witnessed the second highest deforestation rate of any Sumatra province, with approximately 44% of forest cover lost over the last 12 years (World Bank 2001). Today, with population density more than 191 people/km² (Indonesia's Central Bureau of Statistic 2001), Lampung Province is the most densely populated and the poorest province in Sumatra. As a result, remnant forest area in Lampung has declined, with the average forest size declining by a factor of four, and the number of fragments doubling. Burgeoning human populations and the coincident deforestation continue to eliminate wildlife habitat, and what remains is highly fragmented (Hadiprakarsa *et al.* 2007).

Hornbills are a wildlife group of special interest in Asia. With 9 species, the second largest island of Sumatra is the most diverse hornbill island in the country and in the Asia realm. Asian hornbills are the largest frugivorous birds in the tropics. To fulfill their daily energy

requirements, hornbills are able to consume fruits up to 33% of their body weight (Poonswad *et al.* 1998) and are capable of traveling long distance to track fruit resources that are patchily distributed (Tsuji *et al.* 1987, Suryadi *et al.* 1998, Holbrook *et al.* 2002). Compared with other wildlife seed dispersing agents, hornbills disperse large amount of unharmed seeds effectively away from parent trees (Kinnaird 1998, Holbrook and Smith 2000, Wang and Smith 2002). Thus, hornbills play an important role in ecological functions of tropical rainforest by maintaining forest regeneration and may promote forest ecosystem integrity (Kinnaird and O'Brien 2007).

Previous Asian hornbill studies have shown that availability of fruit resources, availability of large trees with suitable nest cavities, and primary forest that can hold their populations are 3 main features necessary for hornbills to survive (e.g., Leighton 1982, Poonswad *et al.* 1988, Kinnaird *et al.* 1996, Kannan and James 1999, Poonswad *et al.* 2000, Datta 2001, Hadiprakarsa and Kinnaird 2004, Kanwatanakid-Savini and Poonswad 2007). Unfortunately, habitat loss and deterioration has reduced current hornbill habitat throughout Asia (Kinnaird and O'Brien 2007). The ability of hornbills to persist in this situation likely varies among species according to habitat needs, landscape configurations, and dispersal abilities (Datta 1998, O'Brien *et al.* 1998, Raman and Mudappa 2003, Sitompul *et al.* 2004, Hadiprakarsa *et al.* 2007, Kinnaird and O'Brien 2007). However, in Indonesia, detailed information on hornbill status, distribution and movement patterns are generally unavailable for most species (Kinnaird and O'Brien 2007). Therefore, conserving hornbills at a broad scale in fragmented landscapes become problematic.

Rapid development of geographic information system (GIS) and remote sensing (RS) technology in few past decades has been critically important for both investigating the habitat

requirements of species and for conservation planning at a broad scale (e.g., Guisan and Zimmermann 2000, Luoto et al. 2002, Linkie et al. 2004, Balaguru et al. 2006). The most common application for this approach is to use species occurrence data to model a species distribution (e.g., Cowley et al. 2000, Austin 2002, Munoz et al. 2005) and habitat requirements (e.g., Brotons et al. 2004, Gibson et al. , Linkie et al. 2007) at a broad scale. Usually, the species distribution data are correlated with a number of environmental predictors (Guisan and Zimmermann 2000, Brotons et al. 2004). However, knowledge of the probability of detecting these species during a survey is important for determining the reliability of predictive model output (Shriner et al. 2006, Linkie et al. 2007). Spatially explicit habitat modeling (SEHM) is one method that has been shown to be a good approach to identify habitat suitability and proportion of occupancy using species occurrences data (Lennon 1999, Palma et al. 1999, Schadt et al. 2002, Linkie et al. 2006).

Logistic regression is a common approach for assessing the relationship between environmental characteristics and species occurrence (Osborne et al. 2001, Bradford et al. 2003, Linkie et al. 2006). However, non-detection of a species at a site does not mean the species is absent, unless detection probabilities are 100% ($P = 1.0$). Therefore, dealing with this type of data can be problematic using ordinary logistic regression due to non-detection error that leads to biased parameter estimation (Gu and Swihart 2004). Thus, MacKenzie et al. (2005) suggested that field researchers collect data and undertake analysis that explicitly incorporates detection probability to reduce these biases.

In this study, we aimed to develop spatially explicit habitat model (SEHM) of Sumatran hornbill probability of occurrence as an approach to identify habitat requirements over a broad

scale that can provide an alternative management tool for hornbill conservation in the fragmented landscape of southern Sumatra, Indonesia.

METHODS

Study area and site selection

Our study was conducted across the southern Sumatra landscape, encompassing approximately 3.5 million ha of land and stretching across the province of Lampung and a small portion in Bengkulu province, (3°45'S and 103°40'E, Figure 1, Chapter 2). The topographical gradient ranges from gentle slopes (<16.5°) to steep slopes (>16.5°), with elevation from 0 to 2200 msl. Forest type ranged from lowland to montane dipterocarp forest. Annual rainfall is generally high, ranging between 2,000 – 4,000 mm and temperature range from 20 – 34° Celsius, although there can be severe droughts during the El Niño Southern Oscillation phenomena (Hedges et al. 2005). Lampung province contains two important protected areas, Bukit Barisan Selatan National Park (BBSNP) and Way Kambas National Park (WKNP). These two national parks serve as a major wildlife refuges for a number of celebrity endangered mammal species, such as Sumatra tiger (*Panthera tigris*), Asian elephant (*Elephas maximus*), Sumatran rhino (*Dicerorhinus sumatrensis*) (Foose and van Strien 1997, Franklin et al. 1999), and more than 200 species of birds (van Marle and Voous 1988, Y. Hadiprakarsa unpublished data).

To identify remnant forest patches, land-cover analysis was carried out by the GIS Department from the WCS Indonesia Program using LANDSAT 7 ETM+ for the year 2000, which had negligible (less than 10%) cloud cover. Classification of land-cover was grouped into forest and non-forest, and used a combination of unsupervised classification and manual interpretation. We defined a forest patch as any closed canopy forest greater than 100 ha and we defined forest patch areas greater than 50,000 ha as source patches. From 60 forest patches

identified, only 34 forest patches met this criterion with only 2 forest patches in the BBSNP complex that qualified as source patches criteria (Table 3.1).

For each forest patch, a series of patch metric variables related to its size and isolation was quantified. We used the Patch Analyst extension version 2.3 for ArcView (Rampel and Carr 2003) to measure patch size and size of nearest neighboring patch. Patch isolation was represented by distance (in km) to the nearest neighbor patch, distance to the source patch and the number of patches that could serve as a stepping stone to the source forest, which were extracted using the Nearest Features extension version 3.8 for ArcView (Jenness 2004). Since many variables were correlated across sites, we used principal component analysis (PCA) to summarize variation in the data set and identify groups with inter-correlated variables to classify forest patches for survey site selections. The PCA results grouped the forest patches into three size classes and two isolation categories: small (< 1,000 ha), medium (1,000 – 5,000 ha) and large (> 5,000 – 50,000 ha), and if the patch was located close (< 5 km) to or far (>5 km) from nearest patches and the source forest.

With roughly an equal number of forest patches in each size and isolation patch groups, we randomly selected 18 from 34 forest patches to be surveyed encompassing approximately 92% of the sampling area in the landscape. Most of the selected forest patches were situated in lowland forest (0 – 500 msl) to hill forest (500 – 1000 msl) with gentle slope (< 16.5°, Table 1), and were under some form of protected management status by provincial or central government, ranging from nature forest reserves to national parks. Only one forest patch had limited production forest status.

Hornbill surveys

Hornbills were surveyed during January to August 2003 in the 18 forest patches across the landscape. We used standard distance sampling (line transect) methods (Buckland *et al.* 2001) to obtain hornbill detection histories for occupancy estimation analysis. A total of 56 line transects was established with numbers and transect length varied according to forest size category (Table 3, Chapter 2). Each transect was walked in the morning (0600-1000) and afternoon (1300-1700) on at least 2 days for each forest patch. The detection of hornbills from visual, vocal or wing beat data, or non-detection, was recorded on each occasion.

Landscape variables

We assessed 5 landscape parameters that we believed had the potential to affect hornbill occurrence: forest patch size (SIZE), mean proximity to settlements (DIVE), public roads (DIRE), elevation (ELEV) and slope (SLOP). Public roads and settlement were digitized from 1:50,000 maps produced by the Indonesian National Coordination Agency for Surveys and Mapping (Bogor, Indonesia) and measured as the Euclidian distance to the nearest transect. Elevation and slope data were obtained from a digital elevation model (DEM) from the NASA Shuttle Radar Topographic Mission (Rabus *et al.* 2003). All spatial predictor variables were converted into 100 m² raster GRID format. We chose 56 sampling points that were randomly selected within each transect. At each sampling point spatial characteristics were extracted and log₁₀ transformed.

Statistical analysis and model design

The best way to assess a predictive model is to test it with independent data collected outside the dataset used to build the model (Fielding 2002); these data were unavailable in this study. Therefore, before we ran the analysis, hornbill occurrence data were partitioned using the

K-fold or 2 partitioning method (Smith ,1994), with randomly and unequally sized groups called the *validation subset* and *training subset* (Smith 1994, Fielding and Bell 1997). Fielding (2002) suggests that the training subset should be larger than the validation subset. To determine the ratio of data partitioning between the *validation subset* and *training subset*, we used heuristic determination (Huberty 1994):

$$R = [1 + (p - 1)^{1/2}]^{-1} \quad (1)$$

where R is the ratio of data partition and p is the number predictors. As a result, on each species, 33% ($n = 19$) of data were used as a validation subset and 67% ($n = 37$) data for training subset.

We used a 3-step process to develop a SEHM of hornbill occurrence in Lampung province. First, we used the software PRESENCE to predict a hornbill detection probability using hornbill detection histories on a subset of the data. Models included detection probability as a constant $p(.)$, or as affected by various combinations of site-specific covariates, such as elevation. Second, results from the best detection probability (p) were incorporated into logistic regression analysis to determine which landscape covariates, individually or in combination, best explained the probability of hornbill presence (ψ). Candidate models from this analysis were ranked by their Akaike Information Criterion (AIC) values (Burnham and Anderson 2002). Third, the best candidate model was used to estimate the probability of patches occupied by each hornbill species. For the final logistic regression model the probability of hornbill occurrence (P) was constructed into a logistic regression model,

$$P = \frac{e(\beta_0 + \sum \beta_i X_i)}{1 + e(\beta_0 + \sum \beta_i X_i)} \quad (2)$$

where β_0 is the constant coefficient (intercept), β_i is a selected independent variable coefficients and X_i represent their associated resultant variables. The prediction maps of hornbill occurrence

were made by loading raster datasets of the predictor variable into ArcGIS 9.2 (ESRI, Redlands, CA) and entering the final model equations into the raster calculator.

Model evaluation

To evaluate model performance and optimum threshold selection from the logistic regression models for each hornbill species, we used area under the receiver operating characteristic curve (AUC) of the receiver operating characteristic (ROC) plots (Fielding and Bell 1997, Cantor et al. 1999). The ROC plot-based approach measures predictive power from predictions (occupied and not occupied) of species distributions (Pearce and Ferrier 2000, Liu et al. 2005), and has shown effectiveness in ecological modeling studies (e.g., Osborne et al. , Schadt et al. 2002, Linkie et al. 2004). To determine the optimum threshold of hornbill presence from SEHM prediction results, we selected the single point in the ROC plots that was closest to the upper-left corner (0,1). Cantor *et al.* (1999) suggest that the point at this corner represents a perfect classification with 100% sensitivity and specificity. ROC plots and AUC were calculated using SPSS software (SPSS 2007), the results are reported as the AUC \pm standard error (SE) and tests that the model results do not differ from chance (i.e., AUC = 0.5). The resultant AUC values range from 0.5 to 1.0, where values above 0.7 indicate an accurate model fit and above 0.9 indicate a highly accurate model (Swets 1988).

RESULTS

From hornbill surveys in 18 forest patches, all 9 Sumatran hornbills were recorded with at least one species recorded in every surveyed forest patch. We observed 366 hornbills on 56 transects with sampling occasions varying from 2 to 8 on each forest patch. Most observed hornbills were identified by calls or wing beats (78%), and only 22% were identified visually. However, because some hornbill species were detected twice or more within a single occasion,

only 216 observations qualified to be used in the analysis. We excluded 5 hornbill species that had small numbers of total occurrences (< 6 occurrence), *B. bicornis*, *A. corrugatus*, *A. galeritus*, *A. albirostris* and *A. malayanus*. As the result, only four common species were used in the final analysis (Table 2).

The majority of our transect sampling was in lowland forest (0 – 500 msl) and hill forest (500 – 1000 msl), with slope terrain that was accessible by observers. Due to study area and logistical limitations, within each forest patch most of our transect sampling points were set up relatively close with an averaged separation < 1 km apart. None of the surveyed forest patches lacked anthropogenic disturbance (Chapter 2) and most of transects were relatively near settlements and public roads (an average of 4.22 km with minimum distance of 0.17 km for proximity to public roads and average of 8.19 km with minimum distance of 1.17 to 26 km for proximity to settlements).

By comparing AIC values of competing models for each species, spatially related gradient covariates, elevation and slopes, were important parameters to explain detection rate of the 3 large-bodied generalist hornbill species, *B. rhinoceros*, *R. vigil* and *R. undulatus*. Probability of occupancy and detection for *B. rhinoceros* were positively related to elevation (ψ (Elev) = 0.87 ± 0.06 , p (Elev) = 0.51 ± 0.06), and were supported with AIC weight > 50% (Table 3.3). Exploring other landscape covariates that reflected habitat disturbance, proximity to roads and settlement, had weak support to explain detection probability of these species. However, probability of occupancy for *R. undulatus* and *A. galeritus* was affected by proximity to settlement with summed Akaike weight nearly 100% (Table 3.3). In contrast, for *A. galeritus*, the only small-bodied territorial species in the analysis, proximity to settlement appeared to influence their detection. Despite the largest detection probability of any of the study species, it

showed the most precision (0.18 ± 0.05 , Model 4.1, Table 3.3). The top ranked result from each species was then used to construct the SEHM of their probability of occurrence across the landscape.

Visual inspection of SEHM model results shows that the importance of proximity to settlement for detecting *A. galeritus* may partly explain occupancy model results. As depicted on the SEHM predictions map (Figure 3.1-A), the higher probability of occurrence of this species was found in areas distant to settlement. Conversely, *B. rhinoceros* and *R. vigil* showed a relatively similar distribution of probability of occurrences in the landscape, which was correlated with landscape terrain (Figure 3.1 B, D). The most generalist and nomadic species, prediction of *R. undulatus* occurrence in the landscape likely showed actual representation of the species occurrence (Figure 3.1-C). Most of the remnant forest patches in the landscape were accessible for this species.

Using optimum threshold values that we selected from ROC plots results (Figure 3.4), the probabilities of presence from SEHM predictions in surveyed and non-surveyed forest patches indicated a similar pattern among hornbill species (Table 3.4 and 3.5). Overall, with the exception of *R. undulatus*, hornbills were predicted to be absent from most non-surveyed patches (Figure 3.2 - A). In contrast, the probability of species being present in surveyed patches was higher (Figure 3.2-B). Forest patches those were larger than 1000 ha and not isolated received a high percentage of the forest patch area that was predicted to be occupied by hornbills (Figure 3.3). From 16 of these forest patches, 11 (Patch ID: 1 - 11) were situated mostly within the Bukit Barisan Selatan Landscape as defined by Gaveau *et al.* (2007). Five forest patches (Patch ID: 12 - 16) were mainly disturbed mangrove forest near Way Kambas National Park. One forest patch

(patch ID 12) nearly disappeared during the study due to heavy encroachments. Therefore, these patches may not really all be potential habitat for hornbills.

Model evaluation of SEHM prediction results indicated that the highest model accuracy was found for the small-bodied territorial species, *A. galeritus*, with 66% of the time random selection from positive group (Sensitivity) will have a score greater than a random selection from negative class (Specificity, Figure 3.3). *B. rhinoceros* and *R. vigil* had 57% and 52% of global model predictions correctly classified, respectively. In contrast, model performance for the most generalist and wide ranging species, *R. undulatus*, was the lowest among hornbill predication models; only 44% from model predictions were correctly classified.

DISCUSSION

Our modeling approach to understanding hornbill occupancy of forest patches in Sumatra provided a diversity of outcomes. Our models generally proved to be noisy and provided some occupancy errors in both directions. That is, we predicted hornbill presence in patches where we did not find them and we found hornbills in patches where we predicted them to not occur. This model noise may be a result of a number of factors. For example, researchers often depend on bold morphological characteristics and loud vocalization and wing beats, hornbills were easy to identify by an observer during surveys. However, these cues may become less obvious when hornbills occupy patchy environments in fragmented landscapes so that the probability of detecting the species is more difficult. In our study, hornbill probability of detection never exceeded 0.5. We suggest that species-specific characteristics related to the appearance and behavior of the species, as well as the local habitat or surrounding landscape, may influence the species detection probability.

The original field data used in the models was developed to attempt distance sampling estimates of hornbill abundance using line transect. Therefore, we did not account for spatial autocorrelation into our model. However, with clustered localization of our sampling points, we suspected that our sampling might not be free from a spatial autocorrelation effect. Ecological studies implicitly assume an underlying spatial pattern in the species distribution and their environment, and there is a tendency of neighboring sample units to possess similar values than would be expected by random chance (Legendre 1993, Smith 1994, Augustin et al. 1998). Lichstein *et al.* (2002) and Betts *et al.* (2006) found that models that ignore the spatial autocorrelation tend to overestimate the importance of environmental variables and could include variables that have little or no relevance. Therefore, to avoid or reduce spatial autocorrelation affects in future modeling studies, we suggest independently evaluating the spatial autocorrelation effect or incorporating it into the model (as autocovariate) to calibrate model performances. Some ecological modeling studies have found, that predictive accuracy and model versatility tend to improve when incorporating an autocovariate term into model development (Legendre 1993, Augustin et al. 1998, Betts et al. 2006).

Model performance and hornbill behavior

With the exception of small-bodied and territorial species, hornbills vary widely in their ability or willingness to cross unsuitable areas in the fragmented landscape (Kinnaird & O'Brien 2007). From the SHEM prediction map results, we showed how nomadic behavior was beneficial for *R. undulatus* to occupy all of the remnant forest patches in the landscape (Figure 3.1-C). Among hornbill species in Asia, the genus *Rhyticeros* is the most widespread, occurring on more oceanic islands than any other genus (Kinnaird & O'Brien 2007). Some incidental observations also recorded that *R. undulatus* was able to cross the 3-km wide Bali strait (van

Ballen *personal communication*.) and was able to cross between forest patches over a densely populated area in the main capital city of Lampung Province (Y. Hadiprakarsa *personal observation*).

Occupancy of *A. galeritus* was influenced by proximity to settlement; we also suggest it is affected by population density. The probability of occupancy of this species was influenced by the availability of large trees, which they need for nesting (Chapter 2). The increase of population density may lead to the removal of large trees through agricultural encroachment or illegal logging to support their livelihood. Kinnaird *et al.* (2003) and Gaveau *et al.* (2007) reported that agricultural encroachment, mostly converted into coffee plantations (O'Brien and Kinnaird 2003), was the most important factor that caused deforestation in Bukit Barisan Selatan National Park and its surroundings. Laurance *et al.* (2002) also found a similar result in the Amazonian rainforest with other species.

For the habitat-restricted species, the model for *A. galeritus* performed better compared to models for the other large-bodied generalist species. Although *B. rhinoceros* and *R. undulatus* have adequate occurrence data compared with the other species, prediction results for these species showed poor agreement with the actual occurrences. Generalist species that occur over a wide range of habitat types are often difficult to model, whereas species that are more limited in habitat utilization are likely to modeled well (Dettmers and Bart 1999, Dettmers *et al.* 2002).

On numerous occasions, a species was predicted to be present in a forest patch but was not observed during surveys; for wide ranging species, this result may reflect their true flexibility to utilize virtually the whole landscape in search of a transient resource that is patchily distributed. This phenomenon also was explained by the density fluctuation for some hornbill species (Kinnaird *et al.* 1996, Anggraini *et al.* 2001). Conversely, species with restricted ranges,

a different result observed, likely due to detection probability being higher. However, when this group of species was confirmed absent from a particular forest patch, it is likely the species was extirpated due to unfavorable causes or some stochastic event.

Our model performances were somewhat below average with respect to AUC index references (Swets 1988). We suspected that our model development strategy using K=2 partitioning method had influenced to the overall model performance. Wiens (2002) suggested that performance of models is related to the tools used to construct or provide information to the models, the data used to drive the models and the internal structure of the model themselves. In addition the partitioning method can influence error rates; consequently, if data are partitioned, the size of training set must be decreased and this can reduce model accuracy (Fielding and Bell 1997, Guisan and Zimmermann 2000).

Our model prediction results were probably affected by the relatively small data set used to build the models and low detection probability. Karl *et al.* (2002) found that error rates of predicting species occurrence with small sample size characterized by high estimates of commission error (when species is predicted to be present in a forest patch but is not observed) and high variability in omission error (when species is predicted to be absent but is observed) estimates. Therefore, to improve model results for future work, we advise evaluating sampling protocol designs for hornbill surveys that can capture more variability in habitat relationships at broad scales. In this case, in accordance with MacKenzie and Royle (2005), for surveying large-bodied, wide-ranging species with large home ranges, we suggesting retain an optimum number of surveyed forest patches but with more repeated surveys. Conversely, for small-bodied species with range restrictions, adding more forest patches to be surveyed will be sufficient to capture more variability for these species.

Conclusions

Our results suggest that acceptable predictive models at the landscape scale can be developed with extra caution on model development strategy. Incidence-based models may be valid for predicting patch occupancies by filled occupancies for non-sampled patches, at the time and place where data were collected. However, this model may fail when used as a forecasting tool to predict future distribution patterns (Castellon and Sieving 2006).

With the large area requirements of suitable habitat for Sumatran hornbills to persist in the landscape, conservation action for these species requires a better understanding of relationships between species and habitat requirements. The lack of such information represents a gap in our knowledge of habitat conservation priorities for hornbills. This study is one of the first to apply spatial explicit modeling to predict probability of occurrence of hornbills in broad scale. Our modeling result showed a great potential of this method to predicting hornbill occurrences.

Application of this model will allow us to improve efficiency of conservation efforts on hornbills. Forest patches, which have not been surveyed for hornbills, can be prioritized to allow for better partitioning of limited conservation resources available. In addition, our model suggests that there should be high probabilities of the species occurrence in some forest patches where they were not detected. This suggests that we should re-survey those sites and if they are truly not present, assessing the potential of conservation priority to the site will be beneficial hornbill management in the future. Therefore, we would recommend further studies for application of spatial explicit modeling approach as an alternative tool for assessing habitat requirements for Sumatran hornbills at broad scales. Furthermore, this tool would be beneficial

aid for land managers to setup conservation priorities for Indonesian hornbills in fragmented landscapes.

LITERATURE CITED

- Anggraini, K., M. F. Kinnaird, and T. G. O'Brien. 2001. The effects of fruit availability and habitat disturbance on an assemblage of Sumatran hornbills. *Bird Conservation International* 10:189-202.
- Augustin, N. H., M. A. Muggleston, and S. T. Buckland. 1998. The role of simulation in modelling spatially correlated data. *Environmetrics* 9:175-196.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modeling* 157:101-118.
- Balaguru, B., S. Britto, N. Nagamurugan, D. Natarajan, and S. Soosairaj. 2006. Identifying conservation priority zones for effective management of tropical forests in Eastern Ghats of India. *Biodiversity and Conservation* 15:1529-1543.
- Betts, M. G., A. W. Diamond, G. J. Forbes, M. A. Villard, and J. S. Gunn. 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecological Modelling* 191:197-224.
- Bradford, D., A. Neale, M. Nash, D. Sada, and J. Jaeger. 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. *Ecology* 84:1012-1023.
- Brotons, L., W. Thuiller, M. Araujo, and A. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27:437-448.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, K. Burnham, and L. Thomas. 2001. *Introduction to Distance Sampling: estimating abundance of biological populations*. Oxford University Press, Oxford.

- Bunnell, F. L. 1999. What habitat is an island ? Pages 1-31 *in* J. Rochelle, L. Lehmann, and J. Wisniewski, editors. Forest fragmentation: wildlife and management implications. Brill, Leiden.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and and multi-model inference. . Second Edition edition. Springer-Verlag, New York, USA.
- Cantor, S., C. Sun, G. Tortolero-Luna, R. Richards-Kortum, and M. Follen. 1999. A comparison of C/B ratios from studies using receiver operating characteristic curve analysis. *Journal of Clinical Epidemiology* 52:885-892.
- Castellon, T. D., and K. E. Sieving. 2006. An Experimental Test of Matrix Permeability and Corridor Use by an Endemic Understory Bird. *Conservation Biology* 20:135-145.
- Cowley, M. J. R., R. J. Wilson, J. L. Leon-Cortes, D. Gutierrez, C. R. Bulman, and C. D. Thomas. 2000. Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *Journal of Applied Ecology* 37:60-72.
- Datta, A. 1998. Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. *Oryx* 32:285-294.
- _____. 2001. An ecological study of sympatric hornbills and fruiting patterns in a tropical forest in Arunachal Pradesh. PhD Dissertation, Saurashtra University, Rajkot, India.
- Dettmers, R., and J. Bart. 1999. A GIS modelling method applied to predicting forest songbird habitat. *Ecological Applications* 9:152-163.
- Dettmers, R., D. A. Buehler, and J. B. Bartlett. 2002. A test and comparison of wildlife-habitat modeling techniques for predicting bird occurrence at a regional scale. Pages 607 - 623 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and

- S. F. B., editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D. C.
- Fielding, A., and J. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38-49.
- Fielding, A. H. 2002. What are the appropriate characteristic of an accuracy measure? Island Press, Washington, D. C., Washington, DC.
- Foose, T. J., and N. van Strien. 1997. Asian Rhinos - Status survey and conservation action plan. IUCN, Gland, Switzerland and Cambridge, UK.
- Franklin, N., Bastoni, Sriyanto, D. Siswomartono, J. Manansang, and R. Tilson. 1999. Last of the Indonesian tigers: a causes for optimism. Pages 130-147 *in* J. Seidensticker, S. Christie, and P. Jackson, editors. *Riding the tiger: Tiger Conservation in Human-dominated Landscapes*. Cambridge University Press, Cambridge, UK.
- FWI/GFW. 2002. The State of the Forest: Indonesia. Forest Watch Indonesia, Bogor, Indonesia and Global Forest Watch, Washington, DC.
- Gaveau, D. L. A., H. Wandono, and F. Setiabudi. 2007. Three decades of deforestation in southwest Sumatra: Have protected areas halted forest loss and logging, and promoted re-growth? *Biological Conservation* 134:495-504.
- Gibson, L., B. Barrett, and A. Burbidge. 2007. Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. *Diversity and Distributions* 13:704-713.
- Greenberg, R. 1996. Managed forest patches and the diversity of birds in southern Mexico. Pages 59-90 *in* J. Schelhas, and R. Greenberg, editors. *Forest Patches in Tropical Landscapes*. Island Press, Washington D.C.

- Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife habitat models. *Biological Conservation* 116:195-203.
- Guisan, A., and N. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147-186.
- Hadiprakarsa, Y., and M. F. Kinnaird. 2004. Foraging characteristics of an assemblage of four Sumatran hornbill species. *Bird Conservation International* 14:S53-S62.
- Hadiprakarsa, Y., M. F. Kinnaird, M. Iqbal, and T. G. O'Brien. 2007. Effects of forest fragmentation on hornbills across the southern Sumatran landscape. Pages 80-91 in *Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4th International Hornbill Conference*. Mabula Game Lodge, Bela-Bela, South Africa.
- Hedges, S., M. J. Tyson, A. F. Sitompul, M. F. Kinnaird, D. Gunaryadi, and Aslan. 2005. Distribution, status, and conservation needs of Asian elephants (*Elephas maximus*) in Lampung Province, Sumatra, Indonesia. *Biological Conservation* 124:35-48.
- Holbrook, K. M., and T. B. Smith. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* 125:249-257.
- Holbrook, K. M., T. B. Smith, and B. D. Hardesty. 2002. Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* 25:745-749.
- Holmes, D. A. 2001. *Deforestation in Indonesia: A Review of the Situation in Sumatra, Kalimantan, and Sulawesi*. World Bank. Jakarta, Indonesia.
- Huberty, C. J. 1994. *Applied discriminant analysis*. John Wiley & Sons. New York, New York.

- Indonesia's Central Bureau of Statistic. 2001. Population Density per Square Kilometer by Province 1971, 1980, 1990, 1995 and 2000 On the World Wide Web:
<http://www.bps.go.id/sector/population/tables.shtml> (Accessed on 12 February 2008)
- Jenness, J. 2004. Nearest features (nearfeat. avx) extension for ArcView 3. x, v. 3.8a Available at, http://www.jennessent.com/arcview/nearest_features.htm.
- Kannan, R., and D. A. James. 1999. Fruiting Phenology and the Conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of Southern India¹. BIOTROPICA 31:167-177.
- Kanwatanakid-Savini, C., and P. Poonswad. 2007. Feeding ecology and food selection of four sympatric hornbill species at Khao Yai National Park, Thailand. Pages 195 *in* Proceedings of The Active Management of Hornbills and their Habitats for Conservation, Proceedings of the 4th International Hornbill Conference. Mabula Game Lodge, Bela-Bela, South Africa.
- Kinnaird, M., and T. G. O'Brien. 2007. The Ecology and Conservation of Asian Hornbills: Farmers of the Forest. The University of Chicago Press, Chicago.
- Kinnaird, M. F. 1998. Evidence for Effective Seed Dispersal by the Sulawesi Red-Knobbed Hornbill, *Aceros cassidix*. BIOTROPICA 30:50-55.
- Kinnaird, M. F., T. G. O'Brien, and S. Suryadi. 1996. Population fluctuation in Sulawesi Red-knobbed Hornbills: tracking figs in space and time. Auk 113:431-440.
- Kinnaird, M. F., E. W. Sanderson, T. G. O'Brien, H. T. Wibisono, and G. Woolmer. 2003. Deforestation Trends in a Tropical Landscape and Implications for Endangered Large Mammals. Conservation Biology 17:245-257.

- Laurance, W., A. Albernaz, G. Schroth, P. Fearnside, S. Bergen, E. Venticinque, and C. Da Costa. 2002. Predictors of deforestation in the Brazilian Amazon. *Journal of Biogeography* 29:737-748.
- Laurance, W. F. 1999. Reflections on the tropical deforestation crisis. *Biological Conservation* 91:109-117.
- Legendre, P. 1993. Spatial Autocorrelation: Trouble or New Paradigm? *Ecology* 74:1659-1673.
- Leighton, M. 1982. Fruit Resources and Patterns of Feeding, Spacing and Grouping Among Sympatric Bornean Hornbills (Bucerotidae). PhD Dissertation, University of California, Davis.
- Lennon, J. J. 1999. Resource selection functions: taking space seriously? *Trends in Ecology & Evolution* 14:399-400.
- Lichstein, J. W., T. R. Simons, S. A. Shriver, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* 72:445-463.
- Linkie, M., G. Chapron, D. Martyr, J. Holden, and N. Leader-Williams. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology* 43:576-586.
- Linkie, M., Y. Dinata, A. Nugroho, and I. A. Haidir. 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. *Biological Conservation* 137:20-27.
- Linkie, M., R. J. Smith, and N. Leader-Williams. 2004. Mapping and predicting deforestation patterns in the lowlands of Sumatra. *Biodiversity and Conservation* 13:1809-1818.
- Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28:385-393.

- Luoto, M., M. Kuussaari, and T. Toivonen. 2002. Modelling butterfly distribution based on remote sensing data. *Journal of Biogeography* 29:1027-1037.
- Mackenzie, D., and J. Royle. 2005. Methodological Insights: Designing Occupancy Studies: General Advice and Allocating Survey Effort. *Journal of Applied Ecology* 42:1105-1114.
- MacKenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi, and L. L. Bailey. 2005. Improving Inferences in Population Studies of Rare Species that Are Detected Imperfectly. *Ecology* 86:1101-1113.
- Mortberg, U. M. 2001. Resident bird species in urban forest remnants; landscape and habitat perspectives. *Landscape Ecology* 16:193-203.
- Munoz, A., R. Real, A. Barbosa, and J. Vargas. 2005. Modelling the distribution of Bonelli's eagle in Spain: implications for conservation planning. *Diversity and Distributions* 11:477-486.
- O'Brien, T. G., and M. F. Kinnaird. 2003. Caffeine and conservation. *Science* 300.
- O'Brien, T. G., M. F. Kinnaird, P. Jepson, and I. Setiawan. 1998. Effect of forest size and structure on the distribution of Sumba Wreathed Hornbills *Aceros everetti*. Pages 209-217 in *Proceedings of The Asian Hornbills: Ecology and Conservation, Proceedings of the Second Asian Hornbill Workshop, Bangkok*.
- Osborne, P. E., J. C. Alonso, and R. G. Bryant. 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology* 38:458-471.
- Palma, L., P. Beja, and M. Rodrigues. 1999. The use of sighting data to analyse Iberian lynx habitat and distribution. *Journal of Applied Ecology* 36:812-824.

- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225-245.
- Poonswad, P., V. Chimchome, K. Plongmai, and P. Chuailua. 2000. Factors influencing the reproduction of Asian Hornbills. Pages 1740-1755 *in* Proceedings of the 22nd International Ornithological Congress. Durban.
- Poonswad, P., A. Tsuji, N. Jirawatkavi, and V. Chimchome. 1998. Some aspect of food and feeding ecology of sympatric species of hornbills species in Khao Yai National Park, Thailand. Pages 137-153 *in* P. Poonswad, editor. *The Asian Hornbills: Ecology and Conservation*. National Center for Genetic Engineering and Biotechnology, Bangkok.
- Poonswad, P., A. Tsuji, and C. Ngarmpongsai. 1988. A comparative ecological study of four sympatric hornbills (Family Bucerotidae) in Thailand. *Acta XIX congressus Internationalis Ornithologi* 2:2781-2791.
- Rabus, B., M. Einder, A. Roth, and R. Balmer. 2003. The shuttle radar topography mission-a new class of digital elevation models acquired by spaceborne radar. *Photogrammetry and Remote Sensing* 57:241-262.
- Raman, T., and D. Mudappa. 2003. Correlates of hornbill distribution and abundance in rainforest fragments in the southern Western Ghats, India. *Bird Conservation International* 13:199-212.
- Rampel, R. S., and A. Carr. 2003. Patch analyst Extension for ArcView 2.3. Available at, <http://flash.lakeheadu.ca/~rrempe/patch/index.html>.
- Sanderson, E. W., K. H. Redford, A. Vedder, P. B. Coppolillo, and S. E. Ward. 2002. A conceptual model for conservation planning based on landscape species requirements. *Landscape and Urban Planning* 58:41-56.

- Schadt, S., E. Revilla, T. Wiegand, F. Knauer, P. Kaczensky, U. Breitenmoser, L. Bufka, J. Cervený, P. Koubek, T. Huber, C. Stanisa, and L. Trepl. 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology* 39:189-203.
- Shriner, S. A., K. R. Wilson, and C. H. Flather. 2006. Reserve networks based on richness hotspots and representation vary with scale. *Ecological Applications* 16:1660-1673.
- Sitompul, A. F., M. F. Kinnaird, and T. G. O'Brien. 2004. Size matters: the effects of forest fragmentation and resource availability on the endemic Sumba Hornbill *Aceros everetti*. *Bird Conservation International* 14:S23-S37.
- Smith, P. A. 1994. Autocorrelation in logistic regression modelling of species' distributions. *Global Ecology and Biogeography Letters* 4:47-61.
- SPSS. 2007. SPSS for Windows Release 16.0.0. *SPSS Inc.*
- Suryadi, S., M. F. Kinnaird, and T. G. O'Brien. 1998. Home ranges and daily movements of the Sulawesi red-knobbed hornbill *Aceros cassidix* during the non-breeding season. Pages 159-170 *in* Proceedings of The Asian hornbills: ecology and conservation. Thai Studies in Biodiversity.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285-1293.
- Tsuji, A., P. Poonswad, and N. Jirawatkari. 1987. Application of radio tracking to study ranging pattern of hornbills (Bucerotidae) in Thailand. Pages 316-351 *in* Proceedings of Proceedings of the Jean Delacour/International Foundation for the Conservation of Birds Symposium on Breeding Birds in Captivity.

- van Marle, J. G., and K. H. Voous. 1988. The birds of Sumatra: an annotated check-list. Pages 1-265 *in* British Ornithological Union Check-list 10. British Ornithological Union, Tring, UK.
- Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology & Evolution* 17:379-385.
- Wiens, J. A. 2002. Predicting species occurrences: Progress, Problems, and Prospects. Pages 739 - 749 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and S. F. B., editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, D. C.
- World Bank. 2001. *Indonesia: Environment and Natural Resource Management in a Time of Transition*. The World Bank. Washington D.C.
- World Resources Institute. 2000. *World Resources*. World Resources Institute. Washington, D.C.

Table 3.1. Spatial statistics of forest patches derived from LANDSAT ETM+ 7 analysis in southern Sumatra landscape, Indonesia, during 2000.

| | Remnant | Candidate | Selected |
|---|-------------------|-------------------|-------------------|
| Patch number | 60 | 34 | 18 |
| Patch size (ha) | | | |
| Min | 0.17 | 153.6 | 153.81 |
| Max | 149,505.19 | 149,505.19 | 149,505.19 |
| Mean | 6,796.84 | 11,962.51 | 20,036.19 |
| ST.Dev | 24,109.30 | 31,051.10 | 40,775.16 |
| Total | 399,989.09 | 398,842.15 | 367,640.41 |
| Nearest patch distance (km) | | | |
| Min | 0.20 | 0.20 | 0.20 |
| Max | 55.94 | 55.94 | 55.94 |
| Mean | 2.30 | 3.72 | 5.55 |
| STDEV | 7.10 | 9.68 | 12.89 |
| Forest area by elevation category (ha)^a | | | |
| Lowland (0 - 500 m dpl) | 195,436.46 | 195105.03 | 175,802.82 |
| Hill (500 - 1000 m dpl) | 123,084.29 | 122,650.20 | 119,888.36 |
| Lower montane (1000 - 1500 m dpl) | 73,046.54 | 72,665.12 | 64,870.17 |
| Upper montane (1500 - 2200 m dpl) | 8,421.80 | 8,421.80 | 7,079.07 |
| Forest area by slope category (ha)^b | | | |
| Gentle slope <16.5 Degree | 315,824.06 | 318,622.22 | 290,622.22 |
| Steep slope >16.5 Degree | 84,165.03 | 80,219.92 | 77,018.19 |

^a Forest by 4 elevation-based categories proposed by van Steenis (1961),

^b Slope categories proposed by Gaveau *et al.* (2007).

Table 3.2. Common and scientific names with weight, territorial, elevation distributions, and home range and daily travels of 4 species of Sumatran hornbills.

| Species ^a | Weight (g) ^b | Territorial ^{b,c} | Elevation distribution (m) ^{b,g} | Home range (km ²) | Daily travel (km) |
|---|-------------------------|----------------------------|---|-------------------------------|----------------------|
| Wreathed hornbill (<i>Rhyticeros undulatus</i>) | 1,950 - 2,515 | no | 0 - 2500 | 28 ^d | > 5 |
| Rhinoceros hornbill (<i>Buceros rhinoceros</i>) | 2,180 - 2,580 | no | 0 - 1000 | ? | 10 – 15 ^d |
| Helmeted hornbill (<i>Rhinoplax vigil</i>) | 2,500 - 3,100 | no | 0 - 1000 | ? | |
| Bushy-crested hornbill (<i>Anorrhinus galeritus</i>) | 933 - 1,172 | yes | 0 - 1800 | 1.5 ^f | < 2.5 ^{c,h} |

^aKemp 2001; ^bKemp 1995; ^cKinnaird and O'Brien 2007; ^dPoonswad and Tsuji 1994; ^eTsuji et al.

1986; ^fWCS-IP Unpublished data; ^gMacKinnon et al. 1993; ^hSimulation result.

Table 3.3. Summary of model selection procedures and parameter estimate to develop models of probability of occurrence for 4 Sumatran hornbills in Lampung Province, Sumatra, Indonesia.

| | Model | AIC | ΔAIC | w | K | -2l | ψ | S.E | p | S.E |
|-------------------------|---------------------------------|------------|-------------------------------|----------|----------|------------|--------------------------|------------|----------|------------|
| <i>1. B. rhinoceros</i> | | | | | | | | | | |
| 1.1 | psi(Elev),p(Elev) | 165.89 | 0 | 0.42 | 4 | 157.89 | 0.87 | 0.06 | 0.51 | 0.06 |
| 1.2 | psi(Elev),p(Elev + Slop) | 167.86 | 1.97 | 0.16 | 5 | 157.86 | | | | |
| 1.3 | psi(Elev),p(Elev + Dive) | 167.88 | 1.99 | 0.15 | 5 | 157.88 | | | | |
| 1.4 | psi(Elev),p(Elev + Dire) | 167.88 | 1.99 | 0.15 | 5 | 157.88 | | | | |
| 1.5 | psi(Elev),p(Elev + Dire + Dive) | 169.83 | 3.94 | 0.06 | 6 | 157.83 | | | | |
| 1.6 | psi(Elev),p(Elev + Slop + Dive) | 169.84 | 3.95 | 0.06 | 6 | 157.84 | | | | |
| 1.7 | psi(Elev),p(Elev + Slop + Dire) | 169.84 | 3.95 | 0.05 | 6 | 157.84 | | | | |
| <i>2. R. vigil</i> | | | | | | | | | | |
| 2.1 | psi(.),p(Slop) | 104.23 | 0 | 0.28 | 3 | 98.23 | 0.41 | 0.10 | 0.47 | 0.07 |
| 2.2 | psi(Elev),p(Slop) | 105.65 | 1.42 | 0.14 | 4 | 97.65 | | | | |
| 2.3 | psi(.),p(Slop + Dire) | 105.96 | 1.73 | 0.12 | 4 | 97.96 | | | | |
| 2.4 | psi(.),p(Elev + Slop) | 106.22 | 1.99 | 0.10 | 4 | 98.22 | | | | |
| 2.5 | psi(.),p(Slop + Dive) | 106.22 | 1.99 | 0.10 | 4 | 98.22 | | | | |
| 2.6 | psi(Dive),p(Slop) | 106.23 | 2 | 0.10 | 4 | 98.23 | | | | |
| 2.7 | psi(Elev),p(Slop + Dire) | 107.19 | 2.96 | 0.06 | 5 | 97.19 | | | | |
| 2.8 | psi(Elev),p(Elev + Slop) | 107.53 | 3.3 | 0.05 | 5 | 97.53 | | | | |
| 2.9 | psi(Elev),p(Slop + Dive) | 107.64 | 3.41 | 0.05 | 5 | 97.64 | | | | |
| 2.10 | psi(.),p(Slop + Dire + Dive) | 107.82 | 3.59 | 0.04 | 5 | 97.82 | | | | |

Notes: ψ is the probability a site is occupied by hornbill species and p is the probability of detecting hornbill in j th survey, Δ AIC is the difference in AIC values between each model with the low model, w is the AIC model weight, K is the number of parameters in the model. (Continued)

Table 3.3. Continued

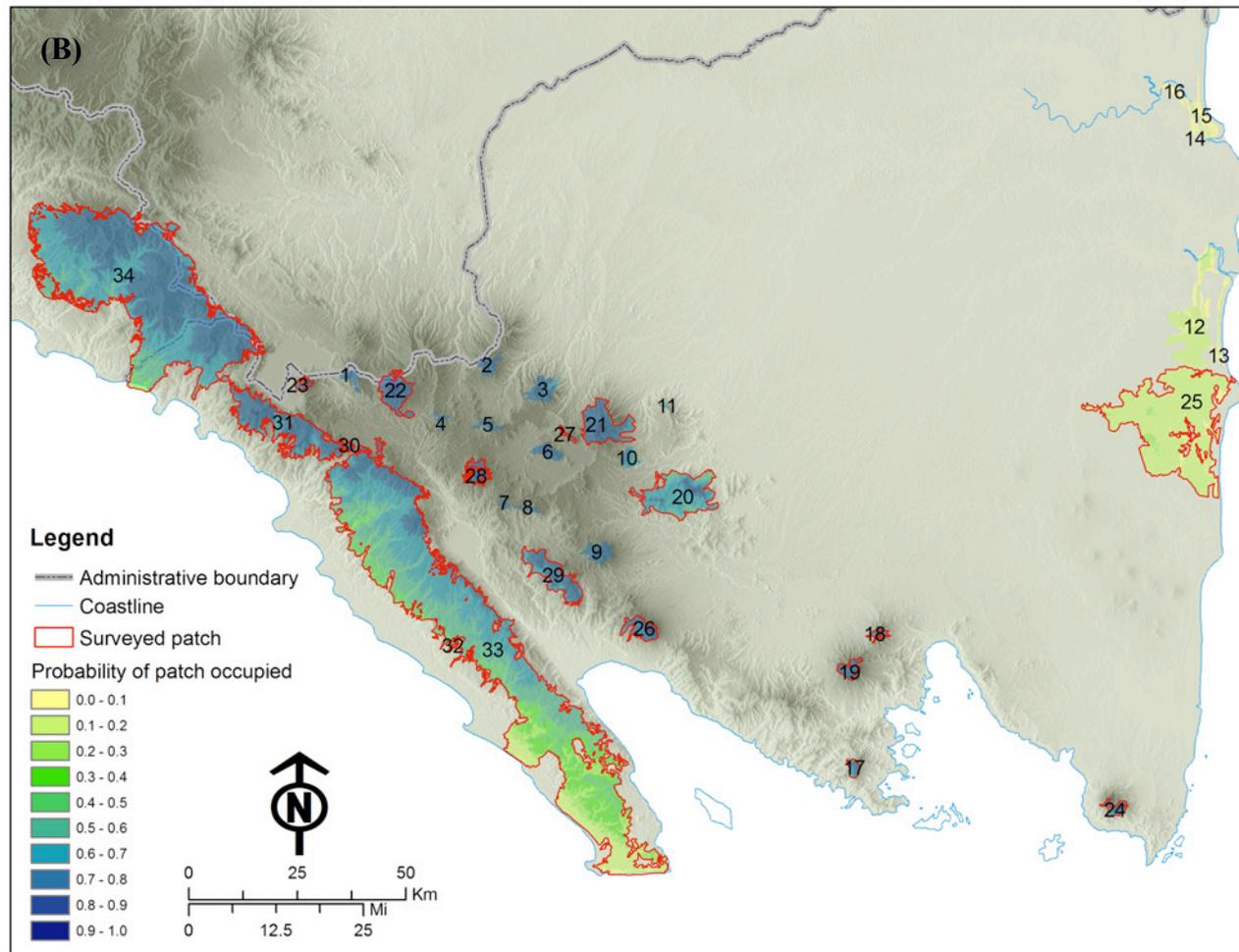
| | Model | AIC | ΔAIC | w | K | -2l | ψ | S.E | p | S.E |
|------------------------|---------------------------------|------------|-------------------------------|----------|----------|------------|--------------------------|------------|----------|------------|
| <i>3. R. undulatus</i> | | | | | | | | | | |
| 3.1 | psi(Dive),p(Elev) | 128.28 | 0 | 0.24 | 4 | 120.28 | 0.63 | 0.13 | 0.29 | 0.08 |
| 3.2 | psi(Dive),p(Dire) | 128.41 | 0.13 | 0.23 | 4 | 120.41 | | | | |
| 3.3 | psi(Dive),p(Dive) | 128.56 | 0.28 | 0.21 | 4 | 120.56 | | | | |
| 3.4 | psi(Dive),p(Elev + Dive) | 130.08 | 1.8 | 0.10 | 5 | 120.08 | | | | |
| 3.5 | psi(Dive),p(Elev + Dire) | 130.27 | 1.99 | 0.09 | 5 | 120.27 | | | | |
| 3.6 | psi(Dive),p(Dive + Dire) | 130.29 | 2.01 | 0.09 | 5 | 120.29 | | | | |
| 3.7 | psi(.),p(Dive) | 131.35 | 3.07 | 0.05 | 3 | 125.35 | | | | |
| <i>4. A. galeritus</i> | | | | | | | | | | |
| 4.1 | psi(Elev),p(Dive) | 116.47 | 0.33 | 0.37 | 4 | 108.47 | 0.79 | 0.11 | 0.18 | 0.05 |
| 4.2 | psi(Elev),p(Elev) | 117.99 | 1.85 | 0.12 | 4 | 109.99 | | | | |
| 4.3 | psi(Elev),p(Slop) | 118.11 | 1.97 | 0.12 | 4 | 110.11 | | | | |
| 4.4 | psi(Elev),p(Dir) | 118.13 | 1.99 | 0.11 | 4 | 110.13 | | | | |
| 4.5 | psi(Elev),p(Elev + Slop + Dive) | 118.83 | 2.69 | 0.08 | 6 | 106.83 | | | | |
| 4.6 | psi(Elev),p(Elev + Dire + Dive) | 119.02 | 2.88 | 0.07 | 6 | 107.02 | | | | |

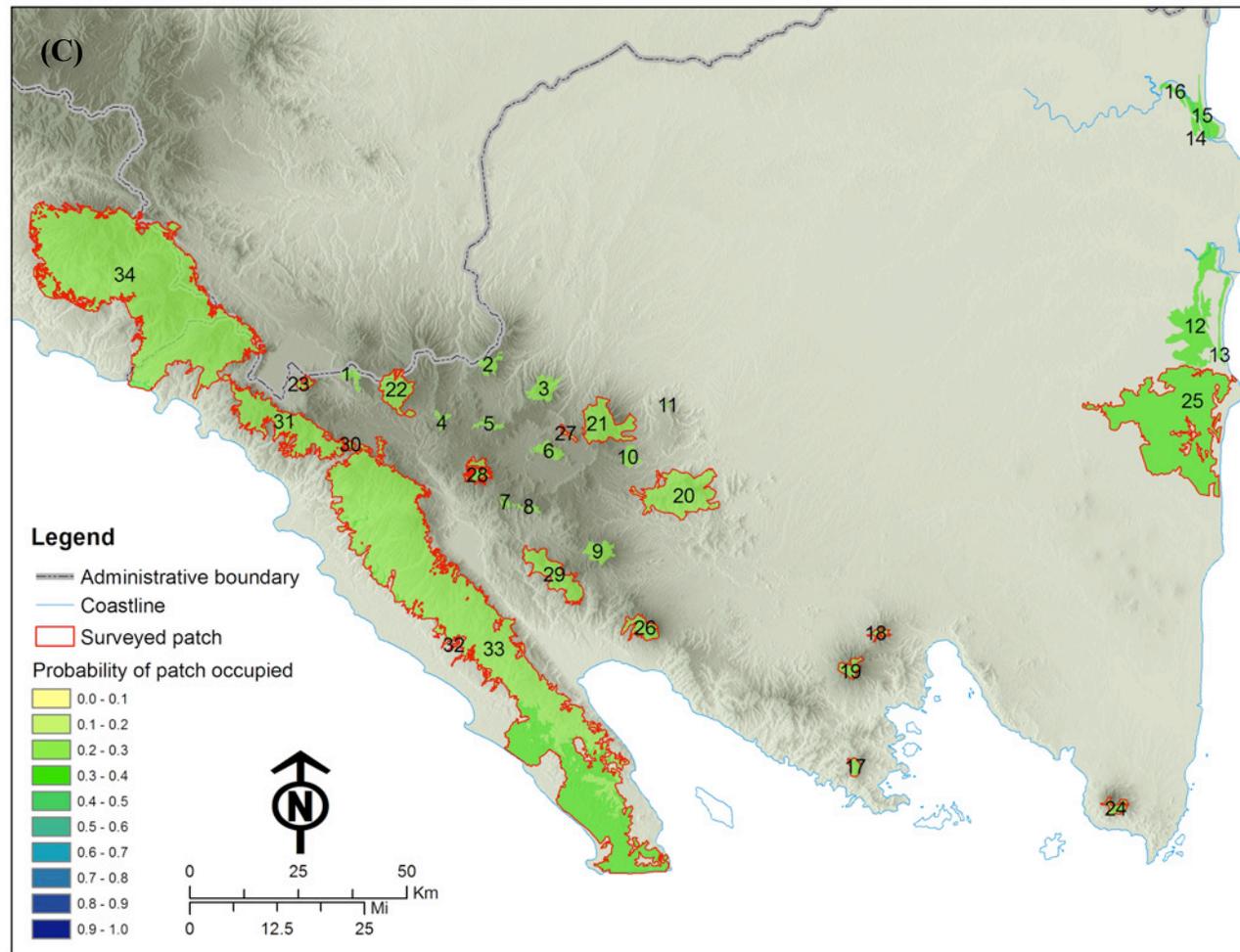
Table 3.4. Predicted mean proportion of patch occupancy and hornbill occurrences in non-surveyed forest patch of four hornbill species in Lampung Province, Sumatra, Indonesia. Note: AG = *A. galeritus*, BR = *B. rhinoceros*, RU = *R. undulatus*, RV = *R. vigil*.

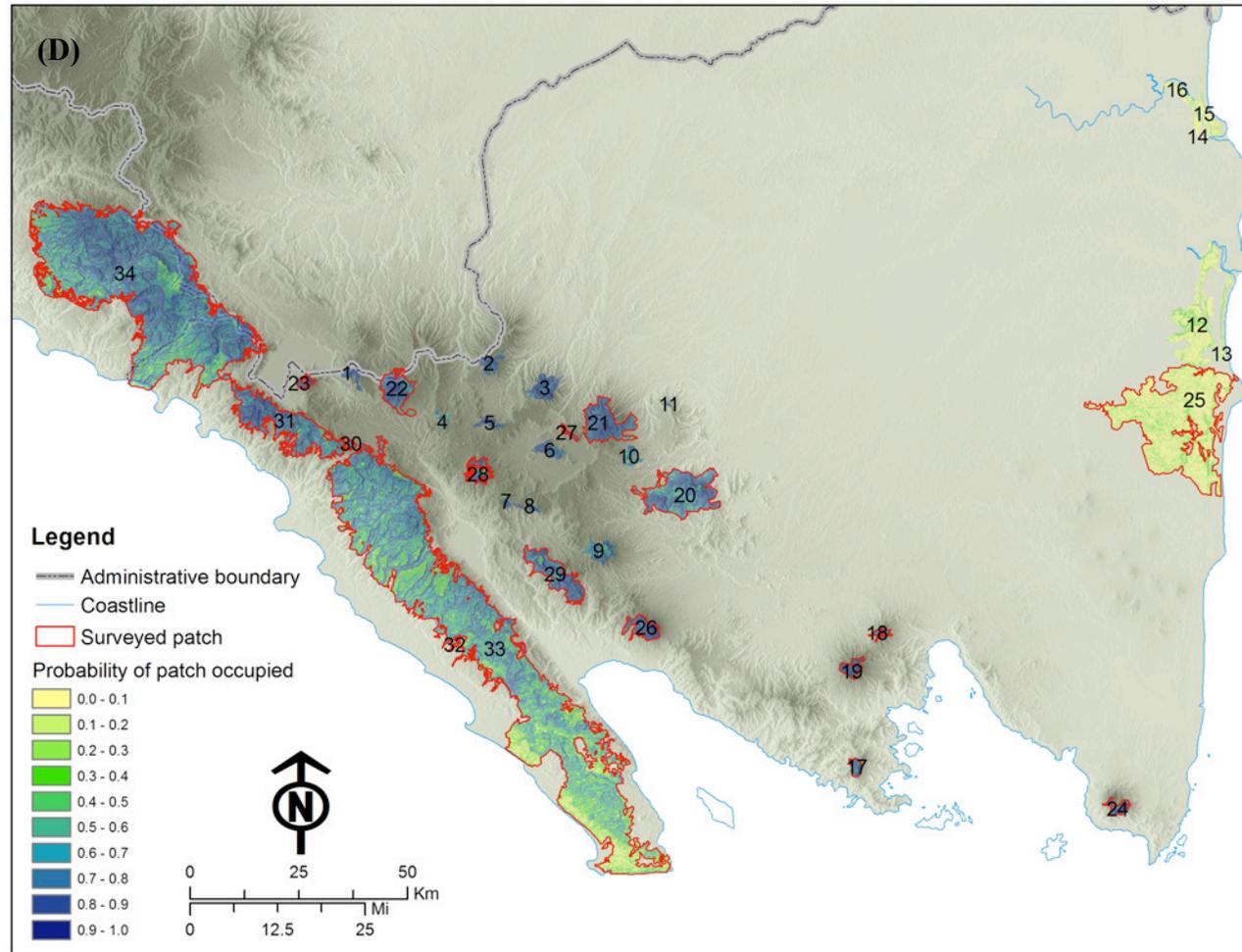
| Patch Id | Patch size | Patch isolation | Predicted mean proportion of patch occupied | | | | Predicted hornbill occurrence | | | |
|----------|------------|-----------------|---|------|------|------|-------------------------------|----|----|----|
| | | | AG | BR | RU | RV | AG | BR | RU | RV |
| 1 | Medium | Not-isolated | 0.15 | 0.44 | 0.16 | 0.48 | 0 | 1 | 0 | 0 |
| 2 | Medium | Not-isolated | 0.07 | 0.77 | 0.26 | 0.76 | 0 | 1 | 0 | 0 |
| 3 | Medium | Isolated | 0.07 | 0.77 | 0.26 | 0.75 | 0 | 1 | 0 | 0 |
| 4 | Medium | Not-isolated | 0.20 | 0.75 | 0.26 | 0.87 | 1 | 1 | 0 | 1 |
| 5 | Small | Not-isolated | 0.09 | 0.77 | 0.26 | 0.81 | 0 | 1 | 0 | 0 |
| 6 | Medium | Not-isolated | 0.23 | 0.69 | 0.27 | 0.70 | 1 | 1 | 1 | 0 |
| 7 | Small | Not-isolated | 0.31 | 0.72 | 0.27 | 0.69 | 1 | 1 | 0 | 0 |
| 8 | Small | Not-isolated | 0.22 | 0.46 | 0.29 | 0.63 | 1 | 1 | 1 | 0 |
| 9 | Small | Not-isolated | 0.10 | 0.76 | 0.26 | 0.76 | 0 | 1 | 0 | 0 |
| 10 | Medium | Isolated | 0.15 | 0.79 | 0.26 | 0.80 | 0 | 1 | 0 | 0 |
| 11 | Small | Not-isolated | 0.16 | 0.28 | 0.11 | 0.34 | 0 | 1 | 0 | 0 |
| 12 | Large | Isolated | 0.18 | 0.70 | 0.27 | 0.84 | 0 | 1 | 0 | 1 |
| 13 | Medium | Not-isolated | 0.26 | 0.75 | 0.26 | 0.78 | 1 | 1 | 0 | 0 |
| 14 | Medium | Not-isolated | 0.08 | 0.76 | 0.26 | 0.86 | 0 | 1 | 0 | 1 |
| 15 | Medium | Not-isolated | 0.20 | 0.08 | 0.35 | 0.27 | 1 | 0 | 1 | 0 |
| 16 | Small | Not-isolated | 0.18 | 0.75 | 0.26 | 0.79 | 0 | 1 | 0 | 0 |

Table 3.5. Predicted mean proportion of patch occupancy and hornbill occurrences with observed occurrences in surveyed forest patch of four hornbill species in Lampung Province, Sumatra, Indonesia. Note: AG = *A. galeritus*, BR = *B. rhinoceros*, RU = *R. undulatus*, RV = *R. vigil*. Predicted occurrences are bolded when the model suggested that the species was present but not actually observed, and italicized when the model predicted no occurrence, but we actually found the species to be present.

| Patch Id | Patch size | Patch isolation | Predicted mean proportion of patch occupied | | | | Predicted hornbill occurrence | | | | Observed hornbill occurrence | | | |
|----------|------------|-----------------|---|------|------|------|-------------------------------|----------|----------|----------|------------------------------|----|----|----|
| | | | AG | BR | RU | RV | AG | BR | RU | RV | AG | BR | RU | RV |
| 17 | Small | Isolated | 0.19 | 0.69 | 0.27 | 0.81 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| 18 | Small | Isolated | 0.05 | 0.80 | 0.26 | 0.84 | 0 | 1 | <i>0</i> | 1 | 0 | 1 | 1 | 0 |
| 19 | Medium | Isolated | 0.01 | 0.58 | 0.21 | 0.69 | 0 | 1 | <i>0</i> | 0 | 0 | 1 | 1 | 0 |
| 20 | Large | Isolated | 0.01 | 0.40 | 0.23 | 0.46 | <i>0</i> | 1 | <i>0</i> | <i>0</i> | 1 | 1 | 1 | 1 |
| 21 | Large | Isolated | 0.19 | 0.63 | 0.28 | 0.76 | 0 | 1 | 1 | <i>0</i> | 0 | 1 | 1 | 1 |
| 22 | Medium | Not-isolated | 0.04 | 0.74 | 0.26 | 0.69 | 0 | 1 | <i>0</i> | 0 | 0 | 1 | 1 | 0 |
| 23 | Small | Not-isolated | 0.28 | 0.71 | 0.27 | 0.83 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| 24 | Medium | Isolated | 0.36 | 0.77 | 0.26 | 0.84 | 1 | 1 | <i>0</i> | 1 | 1 | 1 | 0 | 0 |
| 25 | Large | Not-isolated | 0.33 | 0.16 | 0.33 | 0.12 | 1 | <i>0</i> | 1 | 0 | 1 | 1 | 1 | 0 |
| 26 | Medium | Isolated | 0.23 | 0.72 | 0.27 | 0.83 | 1 | 1 | <i>0</i> | 1 | 0 | 1 | 0 | 0 |
| 27 | Small | Isolated | 0.18 | 0.11 | 0.27 | 0.10 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| 28 | Medium | Not-isolated | 0.26 | 0.76 | 0.26 | 0.84 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| 29 | Large | Not-isolated | 0.09 | 0.75 | 0.26 | 0.83 | <i>0</i> | 1 | <i>0</i> | 1 | 1 | 1 | 1 | 1 |
| 30 | Large | Not-isolated | 0.21 | 0.78 | 0.26 | 0.84 | 1 | 1 | <i>0</i> | 1 | 1 | 1 | 0 | 1 |
| 31 | Small | Not-isolated | 0.62 | 0.06 | 0.36 | 0.06 | 1 | <i>0</i> | 1 | <i>0</i> | 1 | 1 | 1 | 1 |
| 32 | Small | Not-isolated | 0.61 | 0.07 | 0.36 | 0.08 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| 33 | Source | Source | 0.48 | 0.07 | 0.36 | 0.07 | 1 | <i>0</i> | 1 | <i>0</i> | 1 | 1 | 1 | 1 |
| 34 | Source | Source | 0.11 | 0.74 | 0.26 | 0.70 | <i>0</i> | 1 | <i>0</i> | <i>0</i> | 1 | 1 | 1 | 1 |







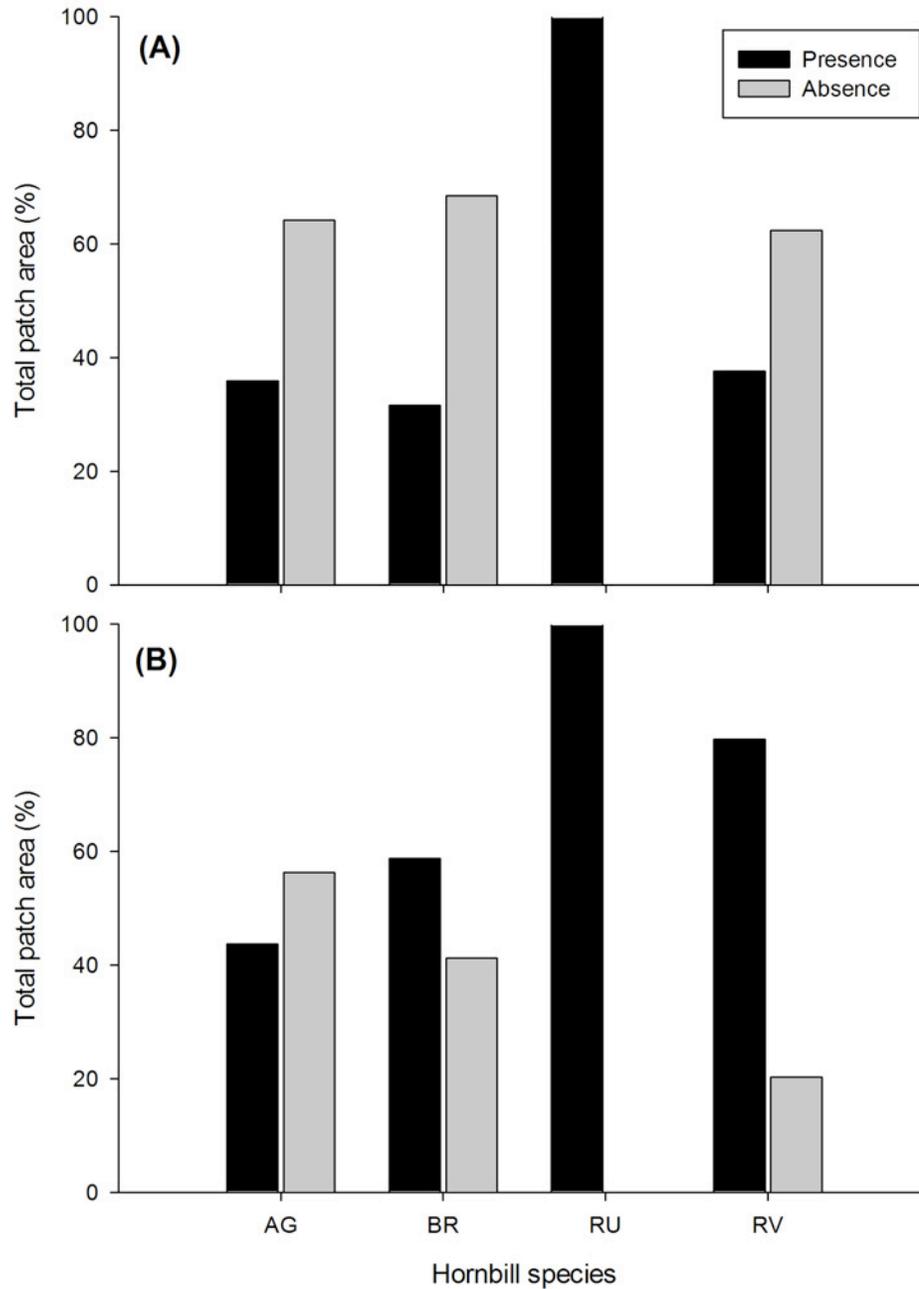


Figure 3.2. Percentage of total patch area of prediction occurrences in non-surveyed (A) and surveyed area (B) for 4 Sumatran hornbills in Lampung Province, Sumatra, Indonesia. Note: AG = *A. galeritus*, BR = *B. rhinoceros*, RU = *R. undulatus*, RV = *R. vigil*.

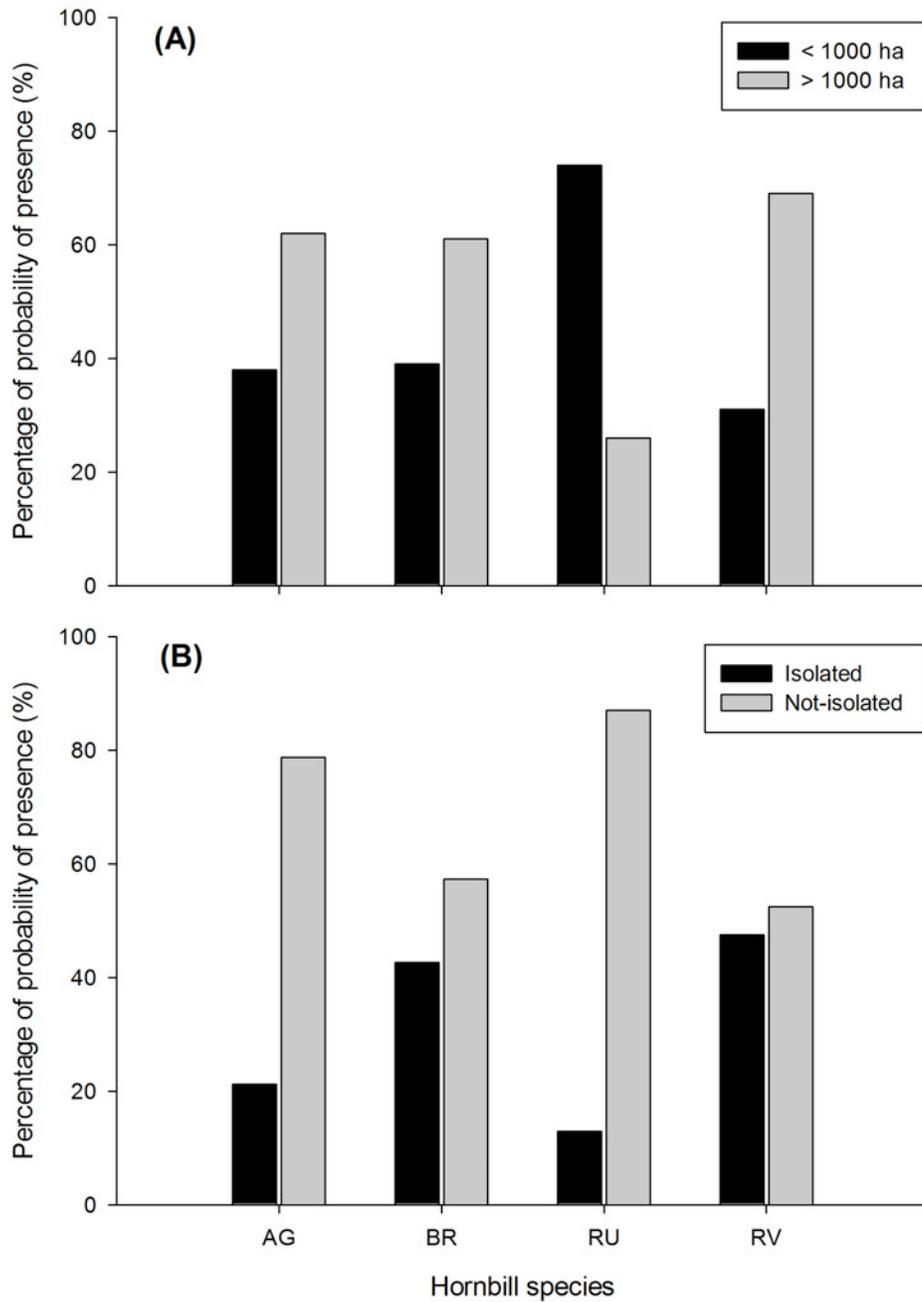


Figure 3.3. Percentage of probability of presences in non-surveyed forest patches. Grouped by forest patch size (A) and forest isolation (B) for 4 Sumatran hornbills in Lampung Province, Sumatra, Indonesia. Note: AG = *A. galeritus*, BR = *B. rhinoceros*, RU = *R. undulatus*, RV = *R. vigil*.

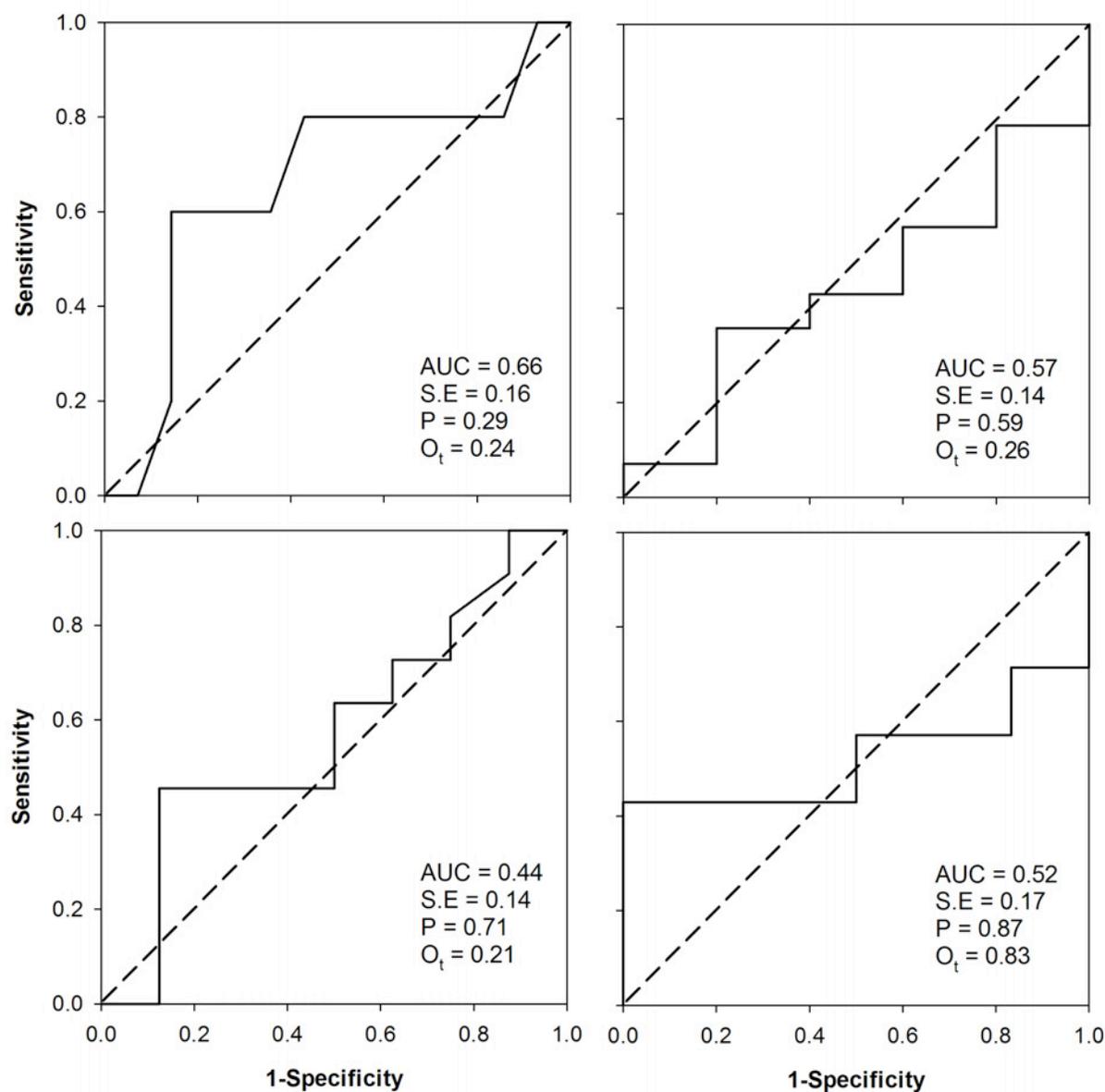


Figure 3.4. Receiver operating characteristic (ROC) plots of developed model of 4 hornbill species. (A) *A. galeritus*, (B) *B. rhinoceros*, (C) *R. undulatus*, (D) *R. vigil*. Note: Diagonal segment produced by ties. S.E was under the non-parametric assumption, P was asymptotic significance with null hypothesis of true area = 0.5. AUC values of > 0.7 is considered good fit and > 0.9 is very good. O_t was optimum threshold selected.

CHAPTER 4

CONCLUSIONS

Important of resource and habitat quality to hornbill occupancy

Occupancy estimation results suggest a positive relationship of resources availability and habitat characteristics, as well as landscape characteristics to the patch occupancy of seven Sumatran hornbills and their detection probability. Fig density and potential nesting tree density were important covariates to patch occupancy estimates for three large-bodied, non-territorial species (*B. rhinoceros*, *B. bicornis* and *R. vigil*) with summed model weights of more than 50%. With movement restriction for small-bodied and territorial species, availability of potential nesting trees was more important for this group of species.

Patch occupancy was higher in low disturbance forest patches for all four hornbill species. Forest patch size was an important covariate to estimate probability of patch occupancy for at least five species of hornbill. In general, patch isolation appeared to not have a strong affect as a covariate to estimate patch occupancy for hornbills. The ability to occupy forest patches was driven by species-specific requirements of resources, habitats and landscape configuration.

The large-bodied non-territorial hornbill species appeared to be more flexible in their ability to occupy forest patches in a fragmented landscape. For small bodied species, distance to the nearest vacant forest patch tends to exceed dispersal abilities, it is likely that the probability

of occupying an isolated patch becomes very low, and their populations may eventually disappear through a combination of stochastic events and habitat loss.

Predicting Sumatran hornbill occurrences

For three large-bodied generalist species, *B. rhinoceros*, *R. vigil* and *R. undulatus*, elevation and slopes, were important parameters to species detection rate. Patch occupancy and detection estimates for *B. rhinoceros* were positively related to elevation. For *R. undulatus* and *A. galeritus*, patch occupancy was affected by proximity to settlement with summed Akaike weight nearly 100%.

Model evaluation of SEHM results showed *A. galeritus*, had the highest accuracy (66%), whereas *B. rhinoceros* and *R. vigil* had 57% and 52% of global model predictions correctly classified, respectively. In contrast, model performance for the most generalist and wide ranging species, *R. undulatus*, was the lowest among hornbill predication models; only 44% from model predictions was correctly classified. Generalist species in this model tend to be difficult to model, whereas species that are more limited in habitat utilization are likely to be modeled well.

Because of clustered localization of our sampling points, we suspected that our sampling might not be free from spatial autocorrelation effects. Therefore, independent evaluation of spatial autocorrelation effects or incorporating these effects into the model (as an autocovariate) may be beneficial to reduce spatial autocorrelation effects. In addition, with low probability of detection over large areas and a relatively small data set used to build the models, these may have also influenced model prediction results.

Because of low detection probability for hornbills, I suggest an improved sampling design protocol for hornbill surveys. For large-bodied, wide-ranging species with large home

ranges, I suggest retaining an optimum number of surveyed forest patches, but with more repeated surveys. Conversely, for small-bodied species with range restrictions, adding more forest patches to be surveyed will be sufficient to capture more variability for these species.

Application of this model showed a great potential of this method to predicting hornbill occurrences and can be used as a tool to improve efficiency of conservation efforts for hornbills. Model results suggest that there should be high probabilities of the species occurrence in some forest patches where they were not detected. If hornbills are truly not present, then the conservation potential of those sites should be assessed for future hornbill management. Furthermore, this tool should be a beneficial aid for land managers to setup conservation priorities for Indonesian hornbill in fragmented landscapes.