



The importance of secondary forest blocks for terrestrial mammals within an *Acacia*/secondary forest matrix in Sarawak, Malaysia

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ABSTRACT

With the rapid conversion of tropical forests in Asia to plantation forests for timber or biofuel production there is a need to determine if these forests serve any viable role in wildlife conservation. We used infra-red trip cameras to survey for large terrestrial mammals within an *Acacia*/secondary forest matrix being created for pulpwood production in Sarawak, Malaysia. We detected at least 27 species of mammals within the matrix and 18 species were detected in both *Acacia* and secondary forest. Using occupancy modeling to determine important covariates for seven mammal species within the project area, six of these species were sensitive to forest type, and most were sensitive to the amount of secondary forest within 1 km of the sample point. For four species (sun bear, *Helarctos melayanus*; common porcupine, *Hystrix brachyura*; mousedeer, *Tragulus* spp.; and pig-tailed macaque, *Macaca nemestrina*), the mean distance of detection from large secondary forest blocks was significantly closer than expected from the distribution of sample points. Most species used *Acacia* forest less frequently than secondary forest, possibly for transit or foraging, with the exception of bearded pigs (*Sus barbatus*), sambar (*Rucervus unicorn*), and civets which were more common in *Acacia* stands. The amount of secondary forest preserved within forest plantations seems to be the best measure of conservation potential for these industrial forests. Forest plantations can provide a conservation value if managed properly and those retaining significant amounts of secondary forest should be eligible for a base level of certification as they comprise a significant portion of the landscape in this region.

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1. Introduction

The global demand for forest products and food production has placed heavy demands on natural forests, especially within the tropics (Foley et al., 2005). In tropical Asia, annual deforestation of humid forests approaches 1% (Achard et al., 2002) and it is estimated Southeast Asia will lose 75% of its native forest by 2100 (Sodhi et al., 2004). Some of this forest will be replaced through reforestation; not with native species, but rather planted industrial forests, including oil palm (*Elais guineensis*), rubber (*Hevea brasiliensis*), *Eucalyptus* (*Eucalyptus* sp.) and *Acacia* (*Acacia* sp.) plantations. The impact of these industrial forests on wildlife populations is of conservation concern (Bennett, 2000; Meijaard et al., 2005).

The island of Borneo is a severe example of forest conditions found throughout the rest of Southeast Asia. Tropical timber extraction from Borneo exceeds that of all tropical wood exports from both tropical Africa and Latin America (ITTO, 2006). According to Curran et al. (2004), 56% of the protected lowland forest in the Kalimantan region of Borneo was lost over a 16-year period (1985–2001) due to legal and illegal logging operations. For the east Malaysian State of Sarawak, approximately 10% of the total land area is planned to be included in Totally Protected Areas (Gumal and Ahmad, 1995). However, many protected areas in Sabah, Sarawak and Kalimantan are already moderately to seriously altered as a result of logging or fires set for purposes of local claims (Curran et al., 2004). With most valuable timber removed from non-protected forests, there has been at least a 40-fold increase in the area designated for oil palm production (Curran et al., 2004). Many Southeast Asian countries, including Malaysia, have undertaken extensive plantings of the fast-growing tree, *Acacia mangium*, to provide a reliable source of pulp and other wood products (Turnbull et al., 1998). Plantations have the potential to supplement degraded tropical forests, but usually the use of exotic

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species and lack of attention to retaining corridors and refugia limit their effectiveness (Lamb, 1998).

Modified forest habitats may lose co-evolved plant and animal species, resulting in moderate to severe aberrations in community structure (Howard and Dutta, 1995). When habitats are significantly disturbed, they reconfigure into alternative steady states, yielding “unforeseen consequences for wildlife” (Schmitz and Sinclair, 1997). Tropical vertebrate species respond in various ways to forest disturbance, most by declining, but others by increasing in abundance (Johns, 1992; Stuebing, 1994). Nakagawa et al. (2006) found terrestrial small mammals communities in harvested and plantation forests of Sarawak, Malaysia, to be little impacted by forestry activity. Large mammal species may decline but not disappear following disturbance. For example, Linkie et al. (2007) documented the occurrence of the semi-arboreal sun bear (*Helarctos malayanus*) in degraded tropical forests in Sumatra. Whereas estimates of abundance were higher in pristine forest, the broad diet of the bears probably allowed its persistence in less optimal forests (Linkie et al., 2007). Tropical forestry has made significant gains in recognizing which species will be sensitive to disturbance and the best practices to minimize the impact (Meijaard and Sheil, 2008).

As with forest logging, not all species decline following forest conversion to plantations, as some species thrive in the rapid succession of habitats, the mosaic of forest age and type, and the loss of predators and competitors. In oil palm plantations, species that can utilize the palm nuts, such as squirrels (*Callosciurus* spp.), common porcupine (*Hystrix brachyura*), palm civets (*Paradoxurus hermaphroditus*) and bearded pigs (*Sus barbatus*) can be abundant and are often considered pest species by plantation managers. There are no significant seed crops produced from the *Acacia* trees, but during the initial generations of plantings significant understory vegetation persists (Lamb, 1998). Changes in forest structure to more open understory and increased herbaceous cover could also benefit ungulate species such as muntjacs (*Muntiacus* spp.) and sambar (*Rucervus unicolor*).

In addition to human-induced changes in habitat configuration and composition, poaching for bush meat is a serious concern for wildlife species in tropical forests (Bennett, 2000). Ungulates may prefer the forest edges created through timber management, but the roads that accompany management activity may expose them to higher levels of poaching (Bennett, 2000). Secondary forest patches may contain high plant productivity and suitable habitat for many mammal species, but serve as a primary destination for timber employees looking to supplement their income and diet through poaching. A source-sink dynamic between large forest blocks and productive, disturbed habitat can lead to persistent ungulate populations in suboptimal habitat (Novaro et al., 2000; Naranjo and Bodmer, 2007). Animals within the tropics of Brazil differed in their ability to move across a matrix composed of forest fragments embedded in agricultural plots, with the matrix as a selective filter determining which species persist (Gascon et al., 1999). Meijaard and Sheil (2008) found the variable responses of mammal species to logging activity in Borneo to depend on species demographics and ecology. The distribution of wildlife species across a tropical planted forest landscape is a function of both habitat and hunting factors that cannot easily be teased apart. For these reasons, wildlife outcomes from conversion to an *Acacia* forest matrix are not easily predicted.

There are several international organizations that have created certification programs to recognize timber companies that maintain biodiversity within their forests (Forest Stewardship Council, 1996; Bowles et al., 1998; Dennis et al., 2008). These certification programs have several components; one is documenting that wildlife species persist within the intentional forest mosaic. These are forest mosaics because most companies strive to maintain rem-

nants of natural forest and riparian corridors. The management prescriptions of the largest silviculture project within Sarawak's industrial forest calls for about 30% of the existing secondary forests within these plantations to be left as remnants embedded throughout the plantations (Stuebing, 2006), far above the 1% mandated within production forests on Peninsular Malaysia (Putz, 1978). In North American forests, extensive research has determined optimal clear-cut sizes, rotation schedules, and road or fire management policies for many wildlife species (see Hunter, 1999). In the tropical forests, there are no standard configurations of plantation and natural forests that promote wildlife species, but such guidelines are urgently needed (Frumhoff, 1995), and are evolving as forestry companies move from focus on extraction to sustainable management (Dennis et al., 2008; Gardner et al., 2009).

Industry has made some effort to mitigate its activities on wildlife species through control of poaching by employees, conservation education and awareness activities to employees and local villagers, and managing the landscape under their control. Forestry practices can be devised which retain some component of the native biodiversity (Meijaard and Sheil, 2008), but forest managers seeking to conserve wildlife within these altered secondary forests are often missing some species. The conceptual framework for conserving tropical biodiversity within a managed landscape is developing (Gardner et al., 2009), but one missing component is identifying which species are capable of persisting within a managed landscape.

Our objective was to document the use of planted *Acacia* forest by wildlife species still present in the area and to determine if the distribution of animals within the matrix is influenced by the mosaic of the conservation areas and the planted forest. Our hope is to identify configurations of habitat that will allow wildlife species to persist within these heavily managed areas.

2. Study area

This study took place on an *Acacia* plantation 40 km southeast of the city of Bintulu, Bintulu Division, Sarawak, Malaysia (N 0792849–0732614, E 0347303–0306538; Fig. 1). Prior the 20th century, most of Sarawak's landscape was covered by forests, including mixed dipterocarp communities in the lowlands (Stuebing, 2005). Over the last century, these forests have undergone significant changes due to increased shifting agriculture by rural communities and the selective logging of valuable timber species by commercial and government entities (Ichikawa, 2007).

Our study was conducted within the 4900 km² Forest Department of Sarawak's Planted Forests Project, also referred to as the Planted Forest Zone (hereafter referred to as PFZ). Our 644 km² study area within the PFZ included at the time of the study 345 km² of *A. mangium* plantation, 198 km² of secondary forest and 100 km² of shifting agriculture from indigenous people. The PFZ is run by the Forest Department of Sarawak State Government. All plantation operations, including conservation management and research, have been contracted to Grand Perfect Sdn. Bhd (GP). Ultimately, 1800 km² of this plantation will be in timber rotation, with 1100 km² in shifting agriculture and 900 km² in secondary forest. Secondary forest is forest that has been selectively logged in the recent past, and these specific forests had been subject to extraction since the early 1970s (P.W. Ngieng, pers. com.). At the time of this study, approximately 47% of the secondary forest had been clear cut and replanted with *A. mangium* ranging from 1 to 7 years in age. This rapidly growing species can obtain heights >7 m at 3 years of age and reaches >16 m when harvested at 8–10 years (Heriansyah et al., 2007). Understory in this *Acacia* forest is dominated by grass (*Trena* spp., *Cyperus* spp. and *Setaria* spp.)

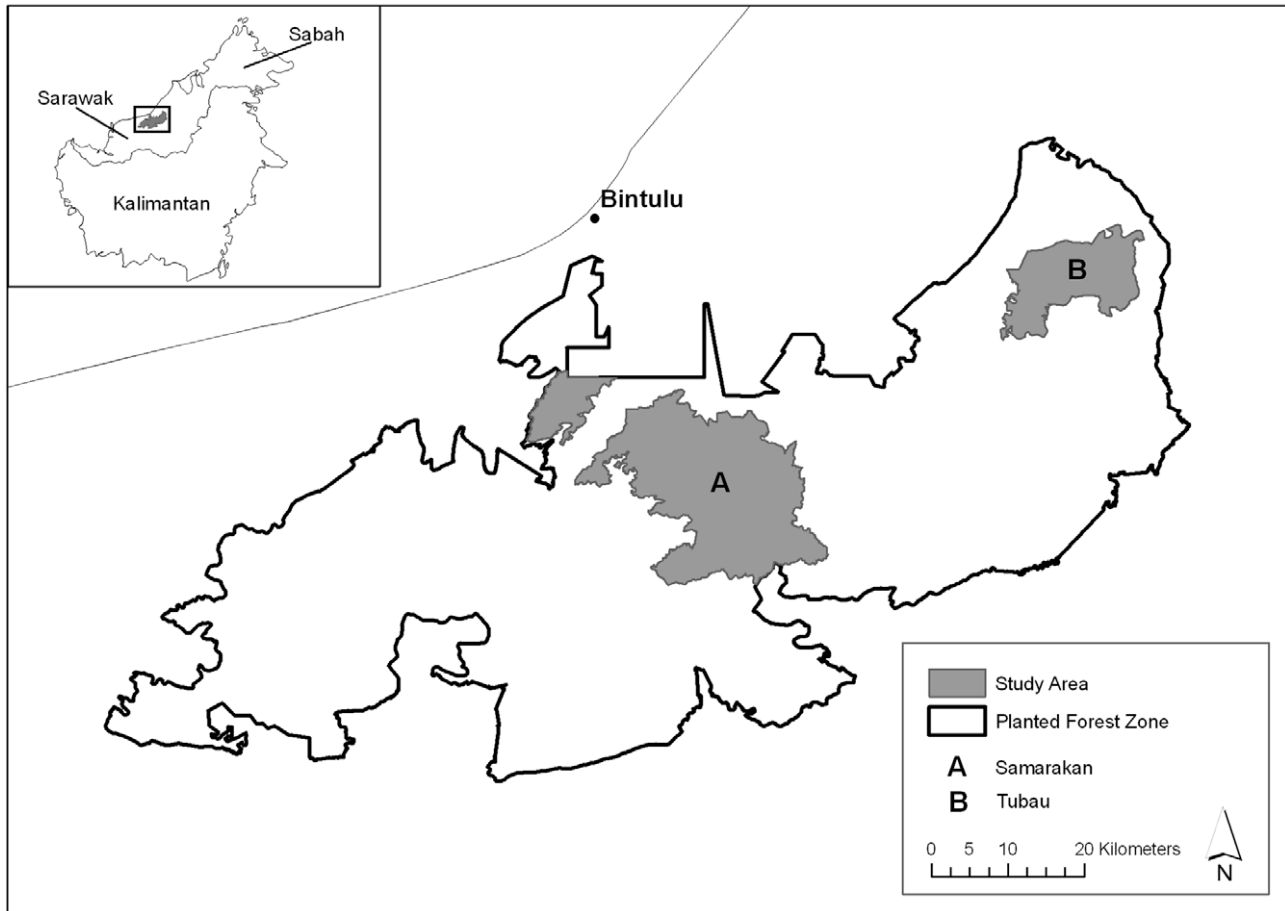


Fig. 1. Location of Planted Forest Zone in Sarawak, and the study area sampled within the Planted Forest Zone. Two study sites within the Planted Forest Zone (Samarakan and Tubau) were sampled from 2005 through 2007.

and ginger (*Etilengera* spp., *Plagiostachys* spp. and *Honstedia* spp.) species (Ragai, 2009). There are two configurations of secondary forest within this plantation: (1) patches of forest, scattered throughout the planted *Acacia* (size range 122 m²–97.4 km²); and (2) narrow corridors (10–100 m wide) following seasonal or perennial streams. Imbedded within the *Acacia* were 13 patches of secondary forest >1 km² ($\bar{X} = 9.70 + 25.4$ SD; range 1–97.4 km²). *Macaranga* spp. and *Calamus* spp. dominate the canopy of the smaller forest patches, with less disturbed patches composed of commercial hardwood species such as *Shorea* spp., *Dipterocarpus* spp., and *Dryobalanops* sp. The understory shrubs in secondary forest include *Melastoma malabathricum*, *Calamus* spp., *Macaranga* spp., *Ficus* spp. and a few from the families of Rubiaceae, Palmae and Gingerberaceae (Ragai, 2009). The remaining 22% of the area (1100 km²) is designated as Native Customary Rights agricultural land. The extensive unplanted portions of these shifting cultivation areas contain many of the same secondary forest tree species, along with ferns, lianas, and wild grasses. *Ficus* spp., *Koompassia excelsa* and *Koompassia malaccensis* are protected as “wildlife trees” throughout the PFZ. For the purposes of this paper we considered agricultural areas to be secondary forest and we only sampled in areas without crops.

3. Methods

3.1. Terrestrial mammal survey

From September 2005 to July 2007, we used commercially available infra-red, remote-trip camera units (DeerCam DC-200;

Non-Typical, Inc., Park Falls, WI, USA) to survey for large mammals within both *Acacia* and secondary forest. Remote-trip cameras have been successfully used to detect predator and ungulate species in the US (Leimgruber et al., 1994; Moruzzi et al., 2002; Swann et al., 2004) and Asia (Numata et al., 2005; Wang et al., 2006). Camera units were positioned approximately 50 cm above the ground, loaded with 400 ASA Fujifilm color print film, and commercial scent lures (Montgomery Fur, Ogden, UT, USA) were applied at least 2.5 m in front of the camera unit as an attractant. Since range of detection is variable in infrared motion sensors due to ambient temperature and body size (Carbone et al., 2001; Swann et al., 2004), we placed the camera unit such that the natural background limited the detection range to <5 m. The camera units were checked after 2 weeks to replace film and batteries and replenish lure. Cameras were left at each location for approximately 30 days. All sites marked using a Global Positioning System (Garmin 60 CS, Olathe, KS, USA).

3.2. Sample points

In 2005 and 2006, sample points were selected within two regions of the plantation (i.e. Samarakan and Tubau), each region was divided into 1 km² blocks and 1–3 camera-units placed within select block. Within each 1 km² block, camera units were placed >200 m apart and 50 m from primary or secondary roads. In 2007, sample points were placed in previously under-sampled regions on the plantation, including the Bukit Mina forest area (see Fig. 2). No camera was placed within 200 m of a previous survey point. We sampled the two types of secondary forest (large tracts

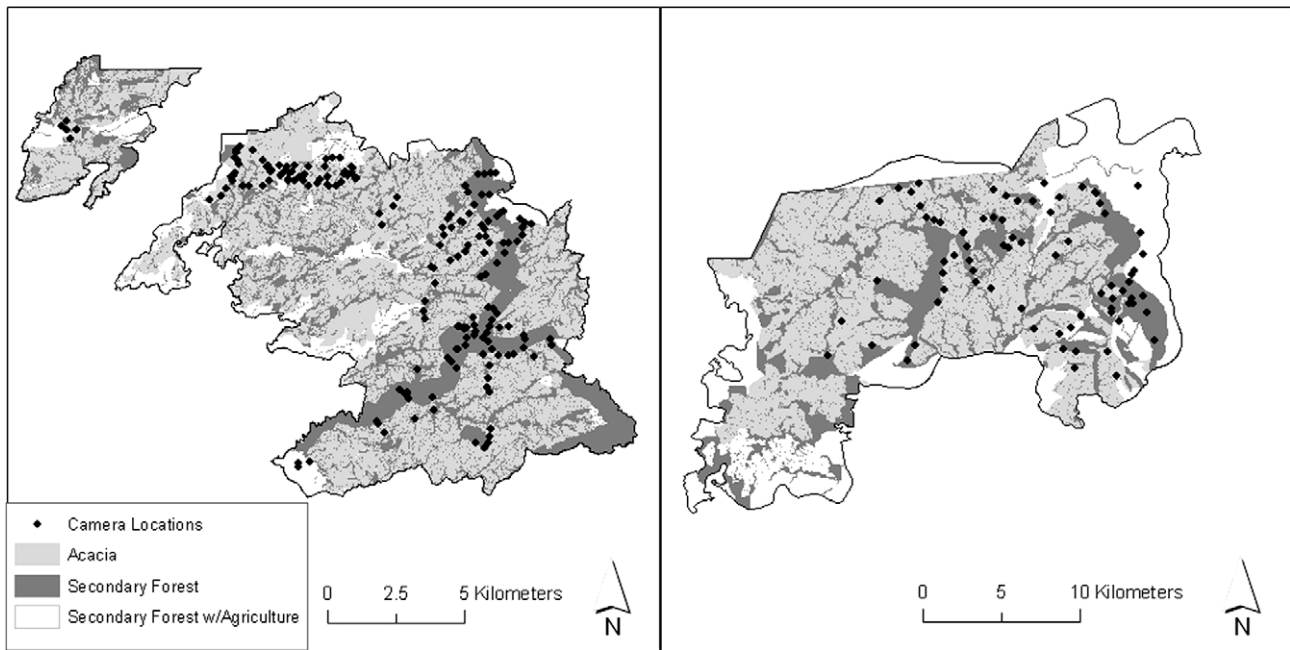


Fig. 2. A map of the study sites (Samarakan on left; Tubau on right) indicating the distribution of sample points within the secondary forest, *Acacia* forest, and shifting cultivation embedded within secondary forest. For the purposes of this paper we considered the shifting cultivation area to be a form of secondary forest.

and corridors), and differentiated between young (1–3 years) and old (4–8 years) *Acacia* plantings, with “old” being stands that exceeded 5 m in height. All *Acacia* plantings were first generation plantings. Our intent was not to estimate mammal densities across the plantation, but to examine the distribution of mammals relative to the secondary forest stands and sample points were selected based on their distance from secondary forest.

4. Data management and analysis

GIS data layers for locations of human settlement (longhouses), roads, land use, and elevation were obtained from GP. Settlement areas and water features were delineated by GP staff, with hand-held GPS units. Monthly rainfall data collected by GP at three locations within the plantation did vary significantly over the study period (range 62–899 mm per month), with higher totals between November and January. We used the data from the weather station closest to the sample location and, for sites sampled across 2 months, we used the rainfall amount from the majority month. Elevation of each sample point was determined using a digital elevation model (DEM) and ranged from 16 to 337 m above sea level.

Since some camera units were expected to fail prior to the end of the 30 day survey, we stepped in front of the camera sensor to trigger a picture during our final collection. If our presence did not trigger the camera, we considered the date of the last picture as the last day the camera unit was operating. We excluded sample points that were sampled for <14 days and the mean sampling period was 26.7 days (range 14–36 days). We created two measures for each sample point: species richness, as the number of species detected at the point; and species detections, as the daily record of an individual species for a survey period. For the smaller species, closely related species could not always be differentiated and the groups are presented at the genus level. For modeling the probability of species occupancy we used only species detected at >13 sam-

ple locations. The daily record of photographs at each location was consolidated into 3 day segments prior to analysis. Occupancy analysis was carried out using Presence 2.0 (MacKenzie et al., 2002; Royle and Nichols, 2003) to determine which sampling (i.e. month, year, and rainfall) and site (i.e. metrics for forest cover, distance to longhouse and river) covariates had the strongest effect on point occupancy for each species in the PFZ (see Table 3). We created two measures of forest cover within 1 km of the sample point: the proportion of secondary forest and the proportion of secondary forest plus older *Acacia* stands. For six large mammal species we obtained sufficient detections to model the occupancy of the animals relative to landscape and habitat features. For three additional groups, mousedeer (*Tragulus kanchil* and *Tragulus napu*), civets/mongoose (*P. hermaphroditus*, *Hemigalus derbyanus*, *Herpestes brachyurus*, *Herpestes smitroquatus*, and *Viverra zangalunga*) and muntjacs, we combined detections from related species prior to analysis, and hereafter refer to the combined groups by their single name. All continuous variables needed to be standardized (0–1) prior to inclusion in the Presence software. All possible combinations of covariates were modeled within Presence and the models ranked in order of Akaike Information Criterion (AIC) values. We examined in more detail all models whose AIC weight was >0.05, and all models ranked within two points of the top model (lowest AIC score) were considered equivalent (Burnham and Anderson, 2002). We created Chi-square tables for each modeled species which was found to be sensitive to secondary forest and tested the distribution of the detections relative to the sampling effort in each forest type. For species richness we included only mammal species with body mass >500 g and used the number of species detected/camera day of operation as our dependent variable within a stepwise (backwards) linear regression. We estimated species richness for *Acacia* and secondary forest using SPECRICH2 (<http://www.mbr-pwrc.usgs.gov/software.html>), which is derived from program CAPTURE and based on an assumption of a closed population with heterogeneous capture probabilities for species (Rexstad and Burnham, 1991).

5. Results

We sampled 212 locations within the study area, including young *Acacia* ($n = 42$), old *Acacia* ($n = 45$), and secondary forest ($n = 125$) (Table 1, Fig. 2). No sample points were without 10% or more secondary forest within a 1 km radius. The proportion of forest cover within 1 km of our sample points increased significantly when we compared secondary forest ($\bar{X} = 0.417 \pm 0.016$) to a combination of secondary forest and older *Acacia* stands ($\bar{X} = 0.738 \pm 0.019$). We conducted 5679 camera trap-nights during September 2005–July 2007. At least 27 mammal species were detected and identified through the camera trapping, and most species were detected in both *Acacia* and secondary forest (Table 2), although there were significantly higher detection rates within secondary forest (paired t -test; $t = 2.37$, d.f. = 26, $p = 0.026$). For the nine mammal species detected in at least 13 locations, we conducted a test for spatial autocorrelation using the two sets of sample points (i.e. Samarakan and Tubau) in 2 km distance bands. Using Moran's I , where values range from 1 (a complete clustering of detections) to -1 (a negative autocorrelation); the range of values obtained (-0.39 to 0.30), and particularly the low values in the closest band (all < 0.091), indicate no significant spatial autocorrelation between detections for each of the focal species (Fortin and Dale, 2005).

Our primary focus was the extent that *Acacia* forest was used by large mammals and whether that use was influenced by the distribution of natural secondary forest patches or corridors. An examination of detection graphs for each species revealed two species (bearded pigs and sambar) to be common in young *Acacia* forest and civet/mongoose to be common in older *Acacia* stands (Fig. 3). Only with civet/mongoose was there evidence that older *Acacia* forest was preferable to young *Acacia* forest (Fig. 3). We conducted a Likelihood ratio χ^2 test for each of these detection graphs and for bearded pigs ($\chi^2 = 2.5$, d.f. = 2, $P > 0.1$), civet/mongoose ($\chi^2 = 2.5$, d.f. = 2, $P > 0.1$) and sambar ($\chi^2 = 1.96$, d.f. = 2, $P > 0.1$) there was no significant deviation from random. For muntjacs ($\chi^2 = 25.2$, d.f. = 2, $P < 0.0001$), mousedeer ($\chi^2 = 9.24$, d.f. = 2, $P = 0.01$), macaques ($\chi^2 = 43.4$, d.f. = 2, $P < 0.001$), thick-spined porcupines ($\chi^2 = 7.22$, d.f. = 2, $P = 0.027$), common porcupines ($\chi^2 = 20.1$, d.f. = 2, $P < 0.0001$) and sun bears ($\chi^2 = 7.48$, d.f. = 2, $P = 0.024$) habitat use was not random.

Differences in detection probability can influence estimates of habitat use for surveys conducted over an extended period (MacKenzie et al., 2002). We used PRESENCE software to account for detection differences in our analysis. The program could not process two species (i.e. sun bears and muntjacs) due to the low number of detections. Models for six of the seven remaining species contained the covariate “forest type” in the final models

Table 1
Summary of habitat qualities and trapping effort within each study area.

Study sites	Area (km ²)	Proportion secondary forest	Proportion shifting agriculture	Mean (m) elevation (range)	Number of sample points ^a	Camera nights
Samarakan	493	0.32	0.12	66 (16–235)	148 (89)	3884
Tubau	151	0.26	0.28	150 (52–337)	64 (36)	1795

^a – Number in parentheses is number of sites within secondary forest.

Table 2
List of species identified (common and scientific name) with proportion of sites where they were detected in 2005–2007.

Species detected		Sample locations	
Common name	Scientific Name	Forest type	
		<i>Acacia</i> ($n = 87$)	Secondary ($n = 125$)
Bearded pig	<i>Sus barbatus</i>	0.26	0.17
Sambar deer	<i>Rucervus unicolor</i>	0.07	0.06
Muntjac species	<i>Muntiacus</i> spp.	0.10	0.22
Lesser mousedeer	<i>Tragulus kanchil</i>	0.0	0.06
Greater mousedeer	<i>Tragulus napu</i>	0.01	0.06
Clouded leopard	<i>Neofelis diardi</i>	0.0	0.01
Marbled cat	<i>Pardofelis marmorata</i>	0.01	0.0
Leopard cat	<i>Prionailurus bengalensis</i>	0.03	0.01
Yellow-throated marten	<i>Martes flavigula</i>	0.01	0.01
Short-tailed mongoose	<i>Herpestes brachyurus</i>	0.03	0.02
Collared mongoose	<i>Herpestes semitorquatus</i>	0.02	0.0
Common palm civet	<i>Paradoxurus hermaphroditus</i>	0.03	0.02
Banded palm civet	<i>Hemigalus derbyanus</i>	0.05	0.02
Malay civet	<i>Viverra zangalunga</i>	0.03	0.06
Tree shrews	<i>Tupaia</i> spp.	0.01	0.05
Pig-tailed macaque	<i>Macaca nemestrina</i>	0.13	0.42
Long-tailed macaque	<i>Macaca fascicularis</i>	0.0	0.02
Thick-spined porcupine	<i>Thacurus crassispinis</i>	0.02	0.09
Common porcupine	<i>Hystrix brachyura</i>	0.03	0.18
Long-tailed porcupine	<i>Trichys fasciculata</i>	0.0	0.05
Sundasciurus squirrels ^a	<i>Sundasciurus</i> spp.	0.0	0.05
Common and Prevost squirrels ^a	<i>Callosciurus</i> spp.	0.01	0.05
Ground squirrels ^a	<i>Lariscus</i> spp.	0.0	0.01
Rats ^a	<i>Muridae</i> spp.	0.05	0.10
Sun bear	<i>Helarctos malayanus</i>	0.01	0.10
Moonrat	<i>Echinosorex gymnurus</i>	0.02	0.01
Otters	<i>Lutra</i> spp.	0.0	0.01

^a Group not included in calculations of species richness.

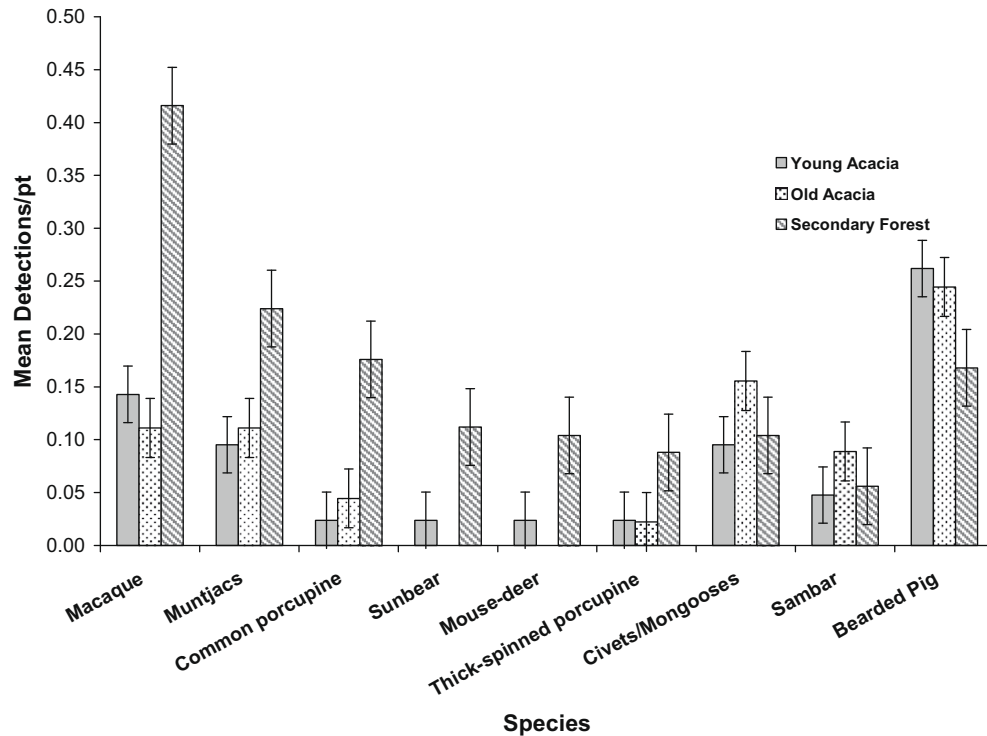


Fig. 3. For nine species with sufficient detections to warrant detection modeling, the rate of detection per sample point for each species in young *Acacia* forest (<4 years of age), old *Acacia* forest (>4 years of age), and secondary forest. The species are arranged from left to right according to their proportional use of secondary and *Acacia* forest.

selected (Table 3, Appendix A), with all species except bearded pigs, civet/mongoose and sambar being less common in *Acacia* forest (Table 2). For four species, the best models also included the amount of secondary forest within 1 km of the survey point, but for only two of these species (i.e. common porcupine and bearded pigs) did the addition of old *Acacia* forest into the calculation of forest cover made a significant contribution to the final models (Table 3). There was no clear pattern observed from the summed model weights of each covariate (Table 4). Secondary forest (with or without including old *Acacia* forest) was not the most important covariate for any species, except for bearded pigs and sambar; both species which were more abundant in *Acacia* forests (Fig. 3).

The distance from our survey points to the closest, large (>1 km²) secondary forest block ranged from 0 to 9827 m (mean 2181 m). The mean distance for detections of four species was significantly closer to secondary forest blocks than random: sun bear ($\bar{X} = 398.07$ m, $Z = 7.13$, $p < 0.001$), mouse deer ($\bar{X} = 733.4$ m, $Z = 2.66$, $p = 0.008$), common porcupine ($\bar{X} = 774.9$ m, $Z = 3.90$, $p < 0.001$), and macaque ($\bar{X} = 1118.4$ m, $Z = 3.62$, $p < 0.001$). For the remaining five species, the distribution was not significantly oriented closer to the secondary forest blocks.

With regards to species richness, the mean number of species detected at secondary forest sites ($n = 125$, $\bar{X} = 1.73 \pm 0.14$ species) was significantly higher than that found at *Acacia* sites ($n = 87$, $\bar{X} = 0.93 \pm 0.129$ species) (z test; $z = 8.87$, $p < 0.001$). Our estimate of species richness within *Acacia* forest (19.9 ± 3.36 species) was lower than that for secondary forest (21.45 ± 3.65 species), but the difference was not significant (z test, $p > 0.1$). A general linear model (stepwise, backwards) contained only two significant variables in the final model; forest type at survey point and the amount of rainfall within the sample period (GLM $F = 6.27$, d.f. = 2, 209, $P = 0.002$). When only secondary forest sites were examined, no variables were significant predictors of species richness (GLM, $P > 0.10$). When we examined only sample points in *Acacia* forest,

distance to the nearest longhouse, the amount of rainfall and elevation were significant predictors of species richness (GLM, $F = 4.88$, d.f. = 3, 83, $P = 0.004$), with distance to longhouse and elevation being positively correlated with the number of species detected.

6. Discussion and conclusions

Although most species were detected in *Acacia* forests, only a limited number of species were found independent of secondary forest patches. Two generalists, bearded pigs and civet/mongoose, appeared to use planted forest more than secondary forest, and an ungulate species, sambar, was common in all forest types. Whether these species can be sustained within an *Acacia* forest, or only persist because of the presence of secondary forest, can only be determined with a productivity study for each species (Naranjo and Bodmer, 2007). The occupancy modeling suggests that sambar, but not bearded pigs or civet/mongoose, are responsive to the amount of secondary forest within the region. This finding indicates the potential for maintaining populations of bearded pigs and civet/mongoose within a monoculture of *Acacia* forest. Sustainable hunting of large mammals is one avenue for conservation money to infuse both local communities and conservation organizations (Robinson and Bodmer, 1999; Bodmer and Robinson, 2004). Subsequent studies should explore the potential to harvest bearded pigs and sambar within an *Acacia* and secondary forest matrix, such as has been done for large mammals in the neotropics (Naranjo and Bodmer, 2007).

While some species can persist within *Acacia* forests, most species were more common in secondary forest and the amount of secondary forest within 1 km of the sample point was a significant factor in their occupancy. Our species list for this matrix included most terrestrial species expected to be found within secondary forest in this region. Our sampling effort (>5600 camera nights) was well beyond the asymptote (approximately 3000

Table 3

Top logistic models for predicting the occupancy of seven mammal species within an *Acacia*/secondary forest matrix in Sarawak, Malaysia in 2005–2007. The models are composed of both occupancy (ψ) and detection (p) covariates. We list all models with an Akaike Information Criterion (AIC) model weight of >0.05 . Twice the negative log likelihood ($-2LL$) is presented for each model, as is the number of parameters (No. par.) estimated occupancy (est. occy.) and estimated detection probability (est. p). The top 20 models from all possible combinations are presented in [Appendix A](#).

Models ^a	Delta AIC	AIC wgt	No. par.	($-2LL$)	est. occy. (± 1 SE)	est. p
<i>Mouse deer</i>						
$\psi(\text{sec, hse}), p(.)$	0	0.1193	4	131.669	0.087 (0.041)	0.251
$\psi(\text{sec, hse}), p(\text{rain, year})$	0.83	0.0788	6	128.496	0.095 (0.051)	0.186
$\psi(\text{for, hse}), p(.)$	0.86	0.0776	4	132.533	0.091 (0.043)	0.242
$\psi(\text{for, sec, hse}), p(.)$	1.36	0.0605	5	131.031	0.088 (0.046)	0.249
$\psi(\text{hse}), p(.)$	1.5	0.0564	3	135.171	0.091 (0.038)	0.245
$\psi(\text{for, hse}), p(\text{rain, year})$	1.54	0.0553	6	129.208	0.100 (0.055)	0.179
<i>Civet</i>						
$\psi(\text{hse}), p(.)$	0	0.1022	3	204.166	0.153 (0.059)	0.170
$\psi(\text{str, hse}), p(.)$	0.9	0.0652	4	203.06	0.151 (0.066)	0.171
$\psi(\text{hse, ag}), p(.)$	0.96	0.0632	4	203.127	0.154 (0.068)	0.170
$\psi(\text{for, hse}), p(.)$	1.17	0.0569	4	203.336	0.152 (0.068)	0.171
<i>Common porcupine</i>						
$\psi(\text{for}), p(\text{year})$	0	0.1860	4	224.299	0.278 (0.107)	0.100
$\psi(\text{for, sec + old}), p(\text{year})$	1.15	0.1047	5	223.451	0.264 (0.117)	0.104
$\psi(\text{for}), p(\text{year, rain})$	1.56	0.0853	5	223.860	0.277 (0.107)	0.101
$\psi(\text{for, str, sec + old}), p(\text{year})$	1.9	0.0719	6	222.202	0.265 (0.132)	0.102
<i>Bearded pigs</i>						
$\psi(.), p(\text{rain, month, year})$	0	0.5031	5	351.415	0.740 (0.206)	0.079
$\psi(\text{for, sec + old, hse}), p(.)$	3.11	0.1063	5	354.5296	0.368 (0.111)	0.160
$\psi(\text{hse, sec + old}), p(.)$	3.87	0.0727	4	357.2909	0.383 (0.109)	0.154
<i>Pig-tailed macaque</i>						
$\psi(\text{for, str, sec}), p(.)$	0	0.2941	5	499.314	0.535 (0.137)	0.168
$\psi(\text{for, str, sec, ag}), p(.)$	1.16	0.1647	6	498.468	0.598 (0.112)	0.149
$\psi(\text{for, str, sec, hse}), p(.)$	1.91	0.1132	6	499.215	0.520 (0.128)	0.173
$\psi(\text{for, str}), p(.)$	2.91	0.0686	4	504.216	0.541 (0.156)	0.166
$\psi(\text{for, str, sec, ag, hse}), p(.)$	3.15	0.0609	7	498.462	0.599 (0.114)	0.149
$\psi(\text{for, sec}), p(.)$	3.24	0.0582	4	504.546	0.534 (0.114)	0.171
<i>Sambar</i>						
$\psi(\text{sec}), p(\text{rain})$	0	0.0741	4	144.134	0.238 (0.148)	0.070
$\psi(.), p(\text{rain})$	0.53	0.0568	3	146.658	0.232 (0.142)	0.070
1 group, Constant P	0.62	0.0543	2	148.750	0.202 (0.126)	0.083
$\psi(\text{sec}), p(.)$	0.66	0.0533	3	146.789	0.198 (0.129)	0.085
<i>Thick-spined porcupine</i>						
$\psi(\text{for}), p(.)$	0	0.0585	3	138.311	0.069 (0.029)	0.296

^a Codes used for covariates: hse – distance (m) to nearest longhouse; str – distance (m) to nearest stream; for – forest type (*Acacia* or secondary) at sample point; sec – % secondary forest within 1 km radius of sample point; sec + old – % forest cover within 1 km radius of sample point if mature *Acacia* considered forest; ag – % agriculture within 1 km radius of sample point; rain – amount of rainfall (mm) during period of survey; month – month of study; year – year of study.

Table 4

For each species, the summed model weight for each occupancy covariate included in models listed in [Table 3](#).

Species	Model variable					
	Secondary forest ^a	Secondary forest and old <i>Acacia</i> ^a	Agriculture ^a	Forest type at survey point	Distance to nearest longhouse	Distance to nearest stream
Mouse deer	0.723	0	0	0.763	1.277	0
Civet sp.	0	0	0.063	0.057	1.083	0.186
Common porcupine	0	0.577	0	1.057	0	0.072
Bearded pig	0	0.179	0	0.106	0.106	0
Macaque	0.427	0	0.226	0.427	0.174	0.702
Sambar	0.127	0	0	0	0	0
Thick-spined porcupine	0	0	0	0.059	0	0

^a Amount within 1 km of survey point.

camera nights) of a species accumulation curve generated in a secondary forest project on mainland Malaysia ([Azlan and Gulam, 2006](#)). [Azlan and Gulam \(2006\)](#) detected 33 species of mammals, but only 27 of these species were photographed. The secondary forest within this plantation matrix was able to maintain a similar number of species (at least 25 detected with

cameras), but we do not know the sustainability of these populations. [Meijaard and Sheil \(2008\)](#) predict species of old phylogenetic age (i.e. specialists) to not persist in forests with high levels of disturbance. [Laurance et al. \(2008\)](#) found large mammal populations in a tropical rainforest still changing over a decade past fragmentation. We recognize that any equilibrium within this

forest matrix may take decades to manifest itself, but from a management standpoint, the potential of maintaining species within a dynamic system is better than attempting to restore lost species. The incorporation of secondary forest within the *Acacia* plantation forest does help to maintain significant mammal diversity over the short-term.

No species preferred young *Acacia* forest, and it was only used by bearded pigs and sambar, even though canopy heights are above 2 m after the second year (Stuebing, pers. observation). With the exception of civet/mongoose, no species were detected more often in older *Acacia* stands; indicating an *Acacia* monoculture of mixed age stands would not be conducive to large mammals and older *Acacia* stands do not serve as an ecological equivalent to secondary forest. In some respects this result is surprising, as the understory within these mature *Acacia* stands was diverse. Aubin et al. (2008) found understory plant communities within temperate plantations to be composed of native species, but in relatively low abundance and diversity. Lamb (1998) noted the importance of understory diversity in maintaining wildlife populations within forest plantations, but he focused on plantations with longer rotation schedules (>50 years) than the 15 years for *Acacia*. We could find no evidence outside of civet species that the age composition of *Acacia* stands was a significant factor in species conservation. Civets may be responding to significant prey densities in *Acacia* forests, although we did not measure this community. Nakagawa et al. (2006) found rodent populations minimally impacted by forest management in a multi-use plantation in Sarawak.

The lack of preference for young or old *Acacia* stands does not mean *Acacia* forests serve no function in large mammal conservation. The detection of at least 20 species of mammals within *Acacia* forests indicate it is used by animals, possibly as transit between secondary forest patches. The lack of significant spatial autocorrelation between detection locations indicates animals were not confined to secondary forest islands and were able to move across the landscape. Of particular note were small felids, which were detected at low levels in all forests. As such, planted forests may be used by these mammals for either foraging or transit to otherwise isolate secondary forest patches. We did not detect an obvious use by terrestrial mammals of the thin corridors of secondary forest maintained along streams. Streamside corridors have proved important to arboreal mammals in other tropical systems (Laurance and Laurance, 1999), but most arboreal mammals were already absent from this system prior to conversion to a plantation.

Quantifying fragmentation within a forest management system is complicated by the relative permeability of the disturbed landscape for the species of concern (Haila, 1999). In the tropics, if secondary forest patches serve to maintain gamma diversity within the human-dominated landscape (Gardner et al., 2009), *Acacia* stands may provide a permeable matrix that allows movement of mammals within meta-populations. Gascon et al. (1999) found most small mammal and bird species moving across an agricultural/secondary forest matrix in Brazil, with many small mammal, but not bird, species persisting in the forest fragments. We detected at least four mammal species that appear to be oriented toward the secondary forest patches, with the sun bear as the best example; its mean detection distance from a large secondary forest block was <400 m. We would assume that these species would not persist within an *Acacia* plantation in the absence of secondary forest blocks. Conserving biodiversity within meta-populations connected through modified habitats may be the only viable solution in human-dense Asia (Pimm and Raven, 2000; Gardner et al., 2009).

Do plantations have a role in wildlife conservation? Recently created plantations, like the one used in this study, do not meet the highest standards of forest stewardship due to a moratorium on certifying new plantations (Forest Stewardship Council, 1996). However, we can use FSC guidelines to assess how well *Acacia* plantations might serve mammal conservation. There are three principles that are pertinent to our study: monitoring wildlife populations, maintaining ecological function, and maintaining High Conservation Value Forest (Forest Stewardship Council, 1996). The camera trap protocols outlined in this study can serve as effective tool in monitoring large mammal populations (Moruzzi et al., 2002; Sanderson and Trolle, 2005). The extensive plantation road system makes for efficient placement and checking of the camera units, and recent advances in monitoring theory compensate for variable detection rates across forest types and ages (MacKenzie et al., 2002). Monitoring both secondary and *Acacia* forest would be important to determine sustainability of the plantation's populations and enable plantation managers to quantify ecological functioning. The persistence of large mammal populations within these plantations can only enhance their potential to sustain functionality. Our results reinforce the importance of High Conservation Value Forest for mammal populations and the need to connect these remnant patches through a configuration of mature *Acacia* stands. The Forest Stewardship Council is correct to discourage continued forest loss and deny new plantations full certification status (Forest Stewardship Council, 1996). However, once that line is crossed, it is counterproductive to acknowledge no conservation value to the remaining forest. We advocate the development of a two-tiered certification process that encourages plantations to retain secondary forest and conduct monitoring activities in order to enhance the plantation's conservation and economic value.

Secondary forest in the tropics has been identified as an important source of timber that might relieve pressure on the logging primary forests (Bawa and Seidler, 1998; Dennis et al., 2008). For most large mammal species, our findings indicate that secondary forest has inherent conservation value as well, and the retention of secondary forest within the plantation forest matrix can be important. Timber managers should not deemphasize or degrade the integrity of these secondary forest blocks. The Bukit Mina Conservation block (97.4 km²) within this project area was a significant size and its conservation value was obvious, but we found mammals throughout the secondary forest patches within the plantation. Mature *Acacia* stands are capable of serving as corridors between these secondary forest patches. With half of the world's wood products currently being derived from plantation forests (FAO, 2007), there is a need to bring these managed forests into a conservation framework. Conservation plans within new plantations should emphasize retention of secondary forest blocks and plantations should be accorded some accreditation for natural forest retention.

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Appendix A

See Table. A1.

Table A1

Top 20 models for each of seven species with sufficient detections. Models are ranked in order of their AIC value with all models within two units of the top model considered equivalent. The codes used for covariates are: hse – distance (m) to nearest longhouse; str – distance (m) to nearest stream; for – forest type (*Acacia* or secondary) at sample point; sec – % secondary forest within 1 km radius of sample point; sec + old – % forest cover within 1 km radius of sample point if mature *Acacia* considered forest; ag – % agriculture within 1 km radius of sample point; rain – amount of rainfall (mm) during period of survey; month – month of study; year – year of study.

Mouse deer Model	AIC	Delta AIC	AIC wgt	Model Likelihood	No. Par.	(–2*Loglike)
psi(hse, sec), p(.)	139.67	0	0.1193	1	4	131.6694
psi(sec, hse), p(rain, year)	140.5	0.83	0.0788	0.6603	6	128.4968
psi(for, hse), p(.)	140.53	0.86	0.0776	0.6505	4	132.5335
psi(for, sec, hse), p(.)	141.03	1.36	0.0605	0.5066	5	131.0314
psi(hse), p(.)	141.17	1.5	0.0564	0.4724	3	135.1712
psi(for, hse), p(rain, year)	141.21	1.54	0.0553	0.463	6	129.2088
psi(str, hse, sec), p(.)	141.52	1.85	0.0473	0.3965	5	131.5234
psi(hse, sec, ag), p(.)	141.64	1.97	0.0446	0.3734	5	131.6437
psi(for, sec, hse), p(rain, year)	141.7	2.03	0.0433	0.3624	7	127.7024
psi(for, str, hse), p(.)	142.09	2.42	0.0356	0.2982	5	132.0908
psi(for, sec + old, hse), p(.)	142.46	2.79	0.0296	0.2478	5	132.4586
psi(sec, hse), p(rain, month, year)	142.49	2.82	0.0291	0.2441	7	128.485
psi(for, ag, hse), p(.)	142.53	2.86	0.0286	0.2393	5	132.5287
psi(for, str, sec, hse), p(.)	142.73	3.06	0.0258	0.2165	6	130.7346
psi(hse, sec + old), p(.)	142.84	3.17	0.0245	0.2049	4	134.8429
psi(for, sec, ag, hse), p(.)	143.03	3.36	0.0222	0.1864	6	131.0267
psi(str, hse), p(.)	143.07	3.4	0.0218	0.1827	4	135.074
psi(hse, ag), p(.)	143.17	3.5	0.0207	0.1738	4	135.168
psi(str, hse, sec, ag), p(.)	143.5	3.83	0.0176	0.1473	6	131.5005
psi(for, str, sec + old, hse), p(.)	143.98	4.31	0.0138	0.1159	6	131.984
<i>Civet model</i>						
psi(hse), p(.)	210.17	0	0.1022	1	3	204.1665
psi(str, hse), p(.)	211.07	0.9	0.0652	0.6376	4	203.069
psi(hse, ag), p(.)	211.13	0.96	0.0632	0.6188	4	203.1278
psi(for, hse), p(.)	211.34	1.17	0.0569	0.5571	4	203.3369
psi(hse, sec + old), p(.)	211.72	1.55	0.0471	0.4607	4	203.7182
psi(str, hse, ag), p(.)	211.92	1.75	0.0426	0.4169	5	201.9236
psi(hse, sec + old, ag), p(.)	211.95	1.78	0.042	0.4107	5	201.952
psi(hse), p(rain)	212.05	1.88	0.0399	0.3906	4	204.0477
psi(for, ag, hse), p(.)	212.11	1.94	0.0387	0.3791	5	202.1052
psi(hse, sec), p(.)	212.15	1.98	0.038	0.3716	4	204.1534
psi(for, str, hse), p(.)	212.35	2.18	0.0344	0.3362	5	202.3475
psi(str, hse, sec + old), p(.)	212.59	2.42	0.0305	0.2982	5	202.5912
psi(str, hse, sec + old, ag), p(.)	212.63	2.46	0.0299	0.2923	6	200.6287
psi(for, sec + old, hse), p(.)	212.94	2.77	0.0256	0.2503	5	202.9413
psi(for, str, ag, hse), p(.)	212.96	2.79	0.0253	0.2478	6	200.9607
psi(str, hse), p(rain)	213.02	2.85	0.0246	0.2405	5	203.0192
psi(str, hse, sec), p(.)	213.03	2.86	0.0245	0.2393	5	203.0272
psi(for, sec + old, ag, hse), p(.)	213.04	2.87	0.0243	0.2381	6	201.0394
psi(hse, sec, ag), p(.)	213.12	2.95	0.0234	0.2288	5	203.1236
psi(for, sec, hse), p(.)	213.21	3.04	0.0223	0.2187	5	203.2147
<i>Common porcupine model</i>						
psi(for), p(year)	232.3	0	0.186	1	4	224.2992
psi(for, sec + old), p(year)	233.45	1.15	0.1047	0.5627	5	223.451
psi(for), p(year, rain)	233.86	1.56	0.0853	0.4584	5	223.8603
psi(for, str, sec + old), p(year)	234.2	1.9	0.0719	0.3867	6	222.2021
psi(.), p(year)	234.98	2.68	0.0487	0.2618	3	228.9776
psi(for, sec + old), p(year, rain)	234.99	2.69	0.0485	0.2605	6	222.9901
psi(for, sec + old), p(.)	235.14	2.84	0.045	0.2417	4	227.1433
psi(for, str, sec + old), p(.)	235.22	2.92	0.0432	0.2322	5	225.2218
psi(for), p(.)	235.83	3.53	0.0318	0.1712	3	229.8321
psi(.), p(rain, year)	236.61	4.31	0.0216	0.1159	4	228.6147
psi(for, sec), p(.)	236.91	4.61	0.0186	0.0998	4	228.9131
psi(for, str), p(.)	236.97	4.67	0.018	0.0968	4	228.9691
psi(for, sec + old, hse), p(.)	236.97	4.67	0.018	0.0968	5	226.9681
psi(.), p(month, year)	236.98	4.68	0.0179	0.0963	4	228.9772
psi(for, sec + old, ag), p(.)	237.04	4.74	0.0174	0.0935	5	227.0406
psi(for, str, sec + old, hse), p(.)	237.14	4.84	0.0165	0.0889	6	225.1363
psi(for, str, sec + old, ag), p(.)	237.2	4.9	0.016	0.0863	6	225.2037
psi(for, ag), p(.)	237.67	5.37	0.0127	0.0682	4	229.6661
psi(for, hse), p(.)	237.81	5.51	0.0118	0.0636	4	229.8052
psi(for, str, sec), p(.)	238.02	5.72	0.0107	0.0573	5	228.0155
<i>Bearded pig model</i>						
psi(.), p(rain, month, year)	361.42	0	0.5031	1	5	351.415
psi(for, sec + old, hse), p(.)	364.53	3.11	0.1063	0.2112	5	354.5296
psi(hse, sec + old), p(.)	365.29	3.87	0.0727	0.1444	4	357.2909

Table A1 (continued)

Mouse deer Model	AIC	Delta AIC	AIC wgt	Model Likelihood	No. Par.	(−2*Loglike)
psi(for, sec + old, ag, hse), p(.)	366.49	5.07	0.0399	0.0793	6	354.4883
psi(.), p(rain, month)	366.56	5.14	0.0385	0.0765	4	358.565
psi(str, hse, sec + old), p(.)	366.8	5.38	0.0342	0.0679	5	356.8036
psi(hse, sec + old, ag), p(.)	367.25	5.83	0.0273	0.0542	5	357.2511
psi(for, hse), p(.)	367.48	6.06	0.0243	0.0483	4	359.4754
psi(hse), p(.)	367.78	6.36	0.0209	0.0416	3	361.7835
psi(for, str, sec + old, ag, hse), p(.)	368.08	6.66	0.018	0.0358	7	354.0828
psi(str, hse, sec + old, ag), p(.)	368.77	7.35	0.0128	0.0253	6	356.7725
psi(for, ag, hse), p(.)	368.94	7.52	0.0117	0.0233	5	358.9446
psi(hse, sec), p(.)	368.99	7.57	0.0114	0.0227	4	360.9893
psi(hse, ag), p(.)	369.28	7.86	0.0099	0.0196	4	361.2767
psi(for, str, hse), p(.)	369.43	8.01	0.0092	0.0182	5	359.4301
psi(str, hse), p(.)	369.73	8.31	0.0079	0.0157	4	361.7275
psi(.), p(month, year)	370.07	8.65	0.0067	0.0132	4	362.0741
psi(hse, sec, ag), p(.)	370.13	8.71	0.0065	0.0128	5	360.1308
psi(.), p(month)	370.35	8.93	0.0058	0.0115	3	364.3489
<i>Pig-tail macaque model</i>						
psi(for, str, sec), p(.)	509.31	0	0.2941	1	5	499.3141
psi(for, str, sec, ag), p(.)	510.47	1.16	0.1647	0.5599	6	498.4681
psi(for, str, sec, hse), p(.)	511.22	1.91	0.1132	0.3848	6	499.2156
psi(for, str), p(.)	512.22	2.91	0.0686	0.2334	4	504.2165
psi(for, str, sec, ag, hse), p(.)	512.46	3.15	0.0609	0.207	7	498.4622
psi(for, sec), p(.)	512.55	3.24	0.0582	0.1979	4	504.5467
psi(for, str, sec + old), p(.)	513.4	4.09	0.0381	0.1294	5	503.3981
psi(for, str, ag), p(.)	514.06	4.75	0.0274	0.093	5	504.0555
psi(for, sec, hse), p(.)	514.1	4.79	0.0268	0.0912	5	504.0987
psi(for, str, hse), p(.)	514.2	4.89	0.0255	0.0867	5	504.2044
psi(for, sec, ag), p(.)	514.28	4.97	0.0245	0.0833	5	504.2773
psi(for, str, sec + old, ag), p(.)	515.39	6.08	0.0141	0.0478	6	503.3911
psi(for, str, sec + old, hse), p(.)	515.39	6.08	0.0141	0.0478	6	503.3944
psi(for, sec, ag, hse), p(.)	515.97	6.66	0.0105	0.0358	6	503.9724
psi(for, str, ag, hse), p(.)	516.05	6.74	0.0101	0.0344	6	504.0538
psi(for), p(.)	516.52	7.21	0.008	0.0272	3	510.5151
psi(str, sec, ag), p(.)	517.21	7.9	0.0057	0.0193	5	507.2095
psi(str, sec), p(.)	517.39	8.08	0.0052	0.0176	4	509.3929
psi(for, str, sec + old, ag, hse), p(.)	517.39	8.08	0.0052	0.0176	7	503.3893
psi(for, ag), p(.)	518.25	8.94	0.0034	0.0114	4	510.2473
<i>Sambar model</i>						
psi(sec), p(rain)	152.13	0	0.0741	1	4	144.1343
psi(.), p(rain)	152.66	0.53	0.0568	0.7672	3	146.6587
1 group, Constant P	152.75	0.62	0.0543	0.7334	2	148.750806
psi(sec), p(.)	152.79	0.66	0.0533	0.7189	3	146.789
psi(for, sec), p(rain)	153.86	1.73	0.0312	0.4211	5	143.8598
psi(for, sec), p(.)	154.11	1.98	0.0275	0.3716	4	146.1094
psi(.), p(rain, year)	154.38	2.25	0.0241	0.3247	4	146.3845
psi(.), p(rain, month)	154.39	2.26	0.0239	0.323	4	146.386
psi(hse), p(.)	154.47	2.34	0.023	0.3104	3	148.4683
psi(.), p(month)	154.55	2.42	0.0221	0.2982	3	148.5489
psi(ag), p(.)	154.58	2.45	0.0218	0.2938	3	148.5826
psi(str), p(.)	154.62	2.49	0.0213	0.2879	3	148.6197
psi(for), p(.)	154.73	2.6	0.0202	0.2725	3	148.7313
psi(.), p(year)	154.74	2.61	0.0201	0.2712	3	148.7403
psi(sec + old), p(.)	154.74	2.61	0.0201	0.2712	3	148.7386
psi(hse, sec), p(.)	154.75	2.62	0.02	0.2698	4	146.7486
psi(sec, ag), p(.)	154.78	2.65	0.0197	0.2658	4	146.779
psi(str, sec), p(.)	154.79	2.66	0.0196	0.2645	4	146.7863
<i>Thick-tailed porcupine Model</i>						
psi(for), p(.)	144.31	0	0.0585	1	3	138.3114
1 group, Constant P	144.98	0.67	0.0419	0.7153	2	140.9833
psi(hse), p(.)	145.08	0.77	0.0398	0.6805	3	139.0771
psi(sec), p(.)	145.11	0.8	0.0392	0.6703	3	139.1115
psi(for, hse), p(.)	145.16	0.85	0.0383	0.6538	4	137.1619
psi(for), p(year)	145.73	1.42	0.0288	0.4916	4	137.7294
psi(.), p(year)	145.76	1.45	0.0284	0.4843	3	139.7567
psi(for, sec), p(.)	145.88	1.57	0.0267	0.4561	4	137.8806
psi(str, sec), p(.)	145.91	1.6	0.0263	0.4493	4	137.9148
psi(str), p(.)	145.92	1.61	0.0262	0.4471	3	139.9231
psi(for, str), p(.)	145.95	1.64	0.0258	0.4404	4	137.9456
psi(for, ag), p(.)	145.97	1.66	0.0255	0.436	4	137.971
psi(for, sec + old), p(.)	146.19	1.88	0.0229	0.3906	4	138.1949
psi(str, hse), p(.)	146.25	1.94	0.0222	0.3791	4	138.2506
psi(hse, sec), p(.)	146.28	1.97	0.0219	0.3734	4	138.2787
psi(hse), p(year)	146.3	1.99	0.0216	0.3697	4	138.2987
psi(sec), p(year)	146.45	2.14	0.0201	0.343	4	138.4463

(continued on next page)

Table A1 (continued)

Mouse deer Model	AIC	Delta AIC	AIC wgt	Model Likelihood	No. Par.	(−2*Loglike)
psi(for, str, hse), p(.)	146.45	2.14	0.0201	0.343	5	136.4452
psi(ag), p(.)	146.63	2.32	0.0184	0.3135	3	140.634
psi(.), p(rain)	146.72	2.41	0.0175	0.2997	3	140.7172

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