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Southeast Asian Primate Communities: Species Richness and Population Density

A Thesis Presented

by

Heather Marie Hassel-Finnegan

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Abstract of the Thesis

Southeast Asian Primate Communities: Species Richness and Population Density

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This thesis studies two aspects of primate diversity in Southeast Asia: species richness and population density. The first chapter investigates the historical and ecological factors that affect primate species richness. The second chapter assesses the reliability of three different methods of determining primate population density.

Patterns of biodiversity are affected by both ecological and historical factors. In Africa and South America, but not Southeast Asia, primate species richness has been found to be positively associated with two proxies for forest productivity: average rainfall and distance from the equator. Southeast Asia's non-conformance may be due to the effect of a) islands, with low colonization and high extinction rates or b) Pleistocene refuges, constricted tropical forests during glacial maxima, which have high present-day species richness. For 45 sites (32 mainland; 13 island), we determined correlations between primate species richness and rainfall, distance from the equator, and several supplementary ecological variables, while controlling for the two aforementioned factors. Results show refuge sites have significantly higher primate species richness than non-refuges (t= -2.76, p<0.05), and distance from refuges is negatively correlated with species richness for non-refuge sites (r= -0.51, p< 0.05). There is no difference in species richness between islands and the mainland (t= -1.4, p= 0.16). The expected positive relationship between rainfall and species richness is not supported (r= 0.17, p=0.28). As predicted, primate species richness is negatively correlated with distance from the equator (r= -0.39, p<0.05) and positively correlated with mean temperature (r= 0.45, p<0.05). General linear models indicate that a site's distance from the equator (F= 6.18, p< 0.05) and Pleistocene refuge classification (F= 5.96, p< 0.05) are the best predictors of species richness. These results suggest that both ecological and historical factors contribute to present day primate species richness in Southeast Asia.

Primate population assessments provide the basis for comparative studies and are necessary prerequisites in determining conservation status. The most widely used

assessment method is line transect sampling which generates systematic data fast and comparatively cheaply. In contrast, the presumably most reliable method is long-term monitoring of known groups, which is both slow and costly. In order to assess the reliability of various analysis methods, we compared group and population densities for white-handed gibbons (*Hylobates lar carpenteri*) and Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) derived from transect walks with those from long-term group follows at Phu Khieo Wildlife Sanctuary, Thailand. A 4-km transect was walked regularly over 30 months (480 km total), resulting in 155 gibbon sightings and 125 leaf monkey sightings. Densities were then estimated using (1) the program DISTANCE, and (2) the Kelker method based on (2.1) perpendicular distances (PD) or (2.2) animal-to-observer distances (AOD). These three estimates were compared to values based on known home ranges, accounting for home range overlap (95% Kernels), combined with group size data. Analyses of line transect data consistently overestimated group densities for both species, while underestimating group size for leaf monkeys. Quality of results varied according to each species group size and spread. However, this study, in accordance with previous studies, found that values derived using AOD (or derivations of this method) matched most closely with population estimates based on home range data.

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The Effects of Ecology and History on Southeast Asian Primate Species Richness

Abstract:

        Patterns of biodiversity are affected by both ecological and historical factors. In Africa and South America, but not Southeast Asia, primate species richness has been found to be positively associated with two proxies for forest productivity: average rainfall and distance from the equator. Southeast Asia's non-conformance may be due to the effect of a) islands, with low colonization and high extinction rates or b) Pleistocene refuges, constricted tropical forests during glacial maxima, which have high present-day species richness. For 45 sites (32 mainland; 13 island), we determined correlations between primate species richness and rainfall, distance from the equator, and several supplementary ecological variables, while controlling for the two aforementioned factors. Results show refuge sites have significantly higher primate species richness than non-refuges (t= -2.76, p<0.05), and distance from the nearest Pleistocene refuge is negatively correlated with species richness for non-refuge sites (r= -0.51, p< 0.05). There is no difference in species richness between islands and the mainland (t= -1.4, p= 0.16). The expected positive relationship between rainfall and species richness is not supported (r= 0.17, p=0.28). As predicted, primate species richness is negatively correlated with distance from the equator (r= -0.39, p<0.05) and positively correlated with mean temperature (r= 0.45, p<0.05). General linear models indicate that a site's distance from the equator (F= 6.18, p< 0.05) and Pleistocene refuge classification (F= 5.96, p< 0.05) are the best predictors of species richness. These results suggest that both ecological and historical factors contribute to present day primate species richness in Southeast Asia.

Introduction:

        Current patterns of biodiversity are determined by a mix of both historical and ecological factors. Historical factors, such as climate change, prehistoric migrations, and continental drift, may influence species distribution and diversification (MacArthur and Wilson 1967; MacArthur 1984; Davis and Shaw 2001). Also, ecological factors, such as forest productivity and food availability may determine whether an area is suitable habitat (Rosenzweig and Abramsky 1993).
        In South America, Africa, and Madagascar, primate species richness is positively correlated with rainfall (Reed and Fleagle 1995), which is often considered to be a predictor of forest productivity (Mittlebach *et al.* 2001). But, this relationship is absent for Asia (Reed and Fleagle 1995). Latitude may also affect forest productivity, as higher levels of solar radiation and less seasonality are expected near the equator. Amongst primates, the expected negative relationship between species richness and distance from the equator is supported in both South America and Africa (Eeley and Lawes 1999; Emmons 1999), but not in Southeast Asia (Emmons 1999). This lack of conformance is potentially related to two major confounding factors.

Island Biogeography
        It has been suggested that the geography of Southeast Asia is a major factor in the region's non-conformance to expected patterns of primate species richness (Reed and Fleagle 1995; Fleagle 1999). The theory of island biogeography hypothesizes that species

richness depends on both the size of a landmass and its distance from a source population (MacArthur and Wilson 1967). Larger landmasses are believed to have greater habitat heterogeneity and more barriers to gene flow, both factors which may affect speciation (Williams 1964). And, areas closer to source populations are expected to have higher rates of immigration then more isolated islands (MacArthur and Wilson 1967).

Primate species-area relationships have been found at a variety of geographic scales. For example, continents with more rainforest area have greater primate species richness then those with less rainforest (Reed and Fleagle 1995). Within both Africa and South America latitudinal gradients in species richness may be associated with species-area relationships (Eeley and Lawes 1999), as equatorial regions have the greatest landmass (Rosenzweig 1995), as well as the greatest species richness (Eeley and Lawes 1999; Emmons 1999). At a finer scale, larger southeast Asian islands have greater primate species richness then small islands (Nijman and Meijaard 2008).

Isolation may also be an important determinant of biodiversity. Isolation affects the rate of immigration, extinction, and speciation (MacArthur and Wilson 1967). The Sunda Shelf islands included in these analyses are classified as land-bridge islands because they were once connected to the mainland (Lawlor 1986) and only became isolated due to recent rises in sea levels about 12,000 years ago (Heaney 1986). Yet, the species-area curve for Sunda shelf islands is significantly lower than the curve for mainland Southeast Asian sites. It is very similar to the curve for Southeast Asian oceanic islands that were separated from the mainland about 160,000 years ago. This indicates that isolation, even recent isolation of land-bridge islands, can have a significant impact on patterns of species richness because of faunal collapses (Heaney 1986). Though, faunal collapse may be limited on the largest of the Sunda shelf land-bridge islands (Heaney 1984).

Pleistocene Refuges

Pleistocene refuges may have also affected the distribution of Southeast Asian primate species (Eudey 1980; Brandon-Jones 1996; Jablonski *et al.* 2000). It has been hypothesized that reduced rainfall during the Pleistocene led to temporary separation of previously continuous rainforests, creating mid-altitude forest patches surrounded by savannah. Forest taxa later re-expanded their ranges during inter-glacial periods (Mayr 1963). As a result, higher species richness has been reported within suspected refuges for both plants and animals (Rodgers *et al.* 1982; Pearson and Carroll 2001; Svenning and Flemming 2007). Some suggest that allopatric speciation occurred within refuges (Colyn *et al.* 1991; Haffer 1997; Abegg and Thierry 2002), though there is controversy as some phylogenies suggest primate speciation predated the Pleistocene epoch (Kay *et al.* 1997; Collins and Dubach 2000).

During the last glacial maximum, there was a significant increase in Southeast Asian montane forest and savannah, with a corresponding decline in rain forest (Heaney 1991). Pollen and termite-community composition analyses indicate that the pattern of rainforest patches that resulted was quite different from that of other continents, in that refuges were abundant, but relatively small and geographically dispersed (Heaney 1991; Gathorne-Hardy *et al.* 2002). In Africa and South America refuges were rare but larger, and concentrated near the equator (Maley 1991; Pennington *et al.* 2000), where primate

species richness is also expected to be high for ecological reasons (Reed and Fleagle 1995; Eeley and Lawes 1999; Emmons 1999).

Purpose of this Study

In addition, to the two factors discussed above, it has also been suggested that the limited sample size of previous studies, and exclusive sampling of only insular and peninsular sites affected the results of previous studies (Reed and Fleagle 1995; Emmons 1999). Here we analyze a large dataset, including insular, peninsular, and mainland sites. We tested for the relationship between species richness and various ecological variables. We also explore explanations for Southeast Asia's non-conformance, including the effects of island biogeography and Pleistocene refuges. We specifically address four questions, related to these topics: a) Do islands have lower species richness than mainland sites? b) Is there a latitudinal gradient in species richness, despite Southeast Asia's small land area near the equator? c) Do suspected refuges have higher species richness than non-refuges? d) Is there a relationship between distance from nearest refuge and species richness?

Methods:

Published and unpublished data from a total of 45 protected areas ($N_{insular}=13$; $N_{continental}=32$; Figure 1.1; Table 1.1) of at least $100km^2$ were included in this analysis (Marsh and Wilson 1981a; Johns 1986, 1988; Tsai 1988; Geissmann 1991; Steinmetz and Mather 1996; Emmons 1999; Gupta and Chivers 1999; Kitayama *et al.* 1999; Blanc *et al.* 2000; Curran and Leighton 2000; Laidlaw 2000; Nhat and Dang 2000; Thinh *et al.* 2000; Ziegler and Herrmann 2000; An and Ziegler 2001; Birdlife 2002; Borries *et al.* 2002; Kinnaird *et al.* 2003; Bunyavejchewin *et al.* 2004; Kanzaki *et al.* 2004; Kitamura *et al.* 2004; Nhan 2004; O'Brien *et al.* 2004; Polet *et al.* 2004; Styring and Hussin 2004; Ziegler *et al.* 2004; Kitamura *et al.* 2005; Yen *et al.* 2005; Anichkin *et al.* 2007; Phiapalath 2007; Vidya *et al.* 2007; Birdlife 2009; UNEP 2009; unpublished data see acknowledgement). The following variables were available for all or most sites: primate species richness, distance from the equator, and rainfall. Wherever possible, data for the following variables was also included: mean temperature, mean minimum temperature, mean maximum temperature, tree density, and number of dry months. All variables were tested for normality, using the Kolmogorov-Smirnov test; all variables were normal (p >0.10). Pearson's r and p-values were calculated for the relationship between primate species richness and all aforementioned variables. All sites that were forested during the last glacial maximum, based on studies of soil, sediments, and plant fossils (Adams 1997), and that are at least 305 m above sea (Maps.com 1999) level were classified as refuges. For all non-refuges we determined the great circle distance to the nearest refuge. Two general linear models were tested. An overall general linear model was not possible, because of correlations between variables. The first general linear model tested the effect of islands, Pleistocene refuges, and rainfall on primate species richness. The second tested the effect of Pleistocene refuges and distance from the equator on primate species richness.

Results:

The relationship between primate species richness and all ecological variables is reported in Table 1.1. Primate species richness is negatively correlated with distance from the equator ($r = -0.39$, $p < 0.05$; Figure 1.2) and positively correlated with mean temperature ($r = 0.45$, $p < 0.05$). Rainfall does not have a significant relationship with species richness ($r = 0.17$, $p = 0.28$), and Lowess localized regression shows no discernable pattern (Figure 1.3). Correlations between species richness and all other variables are not significant: mean maximum temperature ($r = 0.42$, $p = 0.12$); mean minimum temperature ($r = 0.16$, $p = 0.57$); tree density ($r = 0.29$, $p = 0.54$); number of dry months ($r = -0.27$, $p = 0.35$).

Species richness was higher for island then mainland sites, although the difference was not statistically significantly ($t = -1.42$, $p = 0.16$; Figure 1.4). Primate species richness is significantly higher in Pleistocene refuges than non-refuges ($t = -2.76$, $p < 0.05$; Figure 1.5). For non-refuges, the distance to the nearest refuge was negatively correlated with species richness ($r = -0.51$, $p < 0.05$; Figure 1.6)

Results for the general linear models are reported in Table 1.2. The first general linear model found that Pleistocene refuge classification affects species richness ($F = 5.43$, $p < 0.05$), but there is no effect of rainfall ($F = 0.26$, $p = 0.61$) or Island/Continent classification ($F = 0.73$, $p = 0.40$). The second general linear model found that both Pleistocene refuge classification ($F = 5.96$, $p < 0.05$) and distance from the equator ($F = 6.18$, $p < 0.05$) have a significant effect on primate species richness (Figure 1.7).

Discussion:

Our results indicate that distance from the equator, mean temperature, and whether a site served as a Pleistocene refuge are the best predictors of primate species richness in Southeast Asia. Rainfall was not found to be a reliable predictor of primate species richness in the region. And the island effect seemed to have no statistically significant effect on results.

In the past, several hypotheses have been proposed for why rainfall does not predict species richness in Southeast Asia, including: extreme seasonal and year-to-year variation in rainfall, the presence of local low-species-diversity forests dominated by Dipterocarpaceae, and the possibility that high rainfall limits productivity (Reed and Fleagle 1995; Kay *et al.* 1997; Gupta and Chivers 1999). The first hypothesis would predict a lack of relationship between forest productivity and rainfall due to generally similar monsoonal effects across the Southeast Asian region (Kripalani and Kulkarni 1998). The second hypotheses would also predict a lack of relationship between rainfall and forest productivity, due to widescale microhabitat heterogeneity, with dipterocarp areas having uniformly lower primate biomass (Marsh and Wilson 1981b). Meanwhile, the last hypothesis would predict a hill-shaped or saturated curvilinear relationship between forest productivity and rainfall (Kay *et al.* 1997), as rainfall >2500 mm may lead to soil leaching (Richter and Babbar 1991) or reduced photosynthesis because of cloud cover (Raich 1989). According to our results, there is no relationship between rainfall and primate species richness. This makes the first two hypotheses more likely, i.e., seasonal/year-to-year variation in rainfall or the presence of low diversity dipterocarp areas, may explain the lack of relationship between rainfall and primate species richness.

It has been suggested that the island biogeography of Southeast Asia may have complicated past studies of primate communities, which exclusively sampled insular and peninsular sites (Reed and Fleagle 1995; Emmons 1999). Surveys of mammalian fauna on Sunda Shelf islands indicate that low species richness on Southeast Asian islands is more likely due to faunal collapse on very small islands. But, the largest islands, such as those included in our analysis, are marked by low overall levels of mammalian extinction, probably due to high levels of habitat heterogeneity, allowing for niche diversification (Heaney 1984). Our results for primates show a similar pattern, with mean primate species richness actually higher for insular sites than mainland sites (although non-significant). This suggests that the large size of Sumatra and Borneo, in particular, may have limited the island effect.

Latitudinal gradients in species richness are reported amongst a wide range of taxonomic groups (Fernandes and Price 1988; Kaufman 1995; Blackburn and Gaston 1996; Emmons 1999). There are two general causative hypotheses proposed to explain this phenomenon. One suggests that the latitudinal gradient is due to ecological factors. Near the equator, environmental stability, productivity, physical heterogeneity, solar radiation, and temperature are highest, while seasonality and aridity are less extreme. All of these conditions are expected to increase biodiversity (Rohde 1992). The other group of hypotheses suggests that latitudinal gradients are a result of species-area relationships. Most early studies on latitudinal gradients focused on South America and Africa, where the continents are roughly diamond shaped, with the greatest landmass (and species richness) near the equator with land area (and species richness) shrinking towards the poles (Rosenzweig 1995). Our data indicates that there is a strong relationship between distance from the equator and primate species richness in Southeast Asia. This lends support to ecological hypotheses, because the geography of Southeast Asia is not diamond shaped.

For a variety of taxa, species richness is high in sites that served as Pleistocene refuges (Rodgers *et al.* 1982; Pearson and Carroll 2001; Svenning and Flemming 2007) and for non-refuges, decreases according to distance from the nearest refuge (Struhsaker 1981). Debate remains as to whether this is a result of allopatric speciation in isolated forest patches or relic species, which may have been widely distribution before the Pleistocene, but did not re-expand their ranges during post-glacial forest re-expansions (Colyn *et al.* 1991; Fjeldsa and Lovett 1997; Haffer 1997; Collins and Dubach 2000). Southeast Asia has a variety of primate groups that have radiated extensively, including the macaques, hylobatids, and leaf monkeys (Brandon-Jones *et al.* 2004). An incomplete phylogeny of the macaque radiation estimates that speciation events occurred between 1.4-2.2 mya (Hayasaka *et al.* 1996). But, despite some preliminary species-level phylogenies for the hylobatids (Whittaker 2005; Monda *et al.* 2007) and leaf monkeys (Wang *et al.* 1997) there is no clear indication of the timing of intra-family speciation events. Biogeographic evidence supports the possibility of allopatric speciation within refugia (Eudey 1980; Jablonski *et al.* 2000). Our results indicate that Pleistocene refuges have higher primate species richness than non-refuges. For non-refuges, species richness decreases with distance from the nearest refuge. But, it is impossible to decide whether this is the result of allopatric speciation or non-expansion of relic species until more comprehensive phylogenies and information about the timing of speciation events become available for Southeast Asian primates.

Studies of primate communities, such as this one, may help to determine the ecological and historical factors that typify diversity hotspots. Our results indicate that Southeast Asian sites close to the equator and those that served as Pleistocene refugia have the greatest primate species richness. High species richness near the equator may be due to environmental stability, high levels of primary productivity, high levels of solar radiation, and high temperatures. While high species richness in and near Pleistocene refuges suggests that there may have been allopatric speciation of primates within these areas, or relic species that never re-expanded their ranges following the last glacial maximum.

Table 1.1. Complete dataset.

Site	Country	Species Richness	Mean Rainfall (mm)	Latitude	Number Dry Months	Tree Density	Mean Min Temperature	Mean Max Temperature	Mean Temperature	Island/Penninsula	Refuge	Distance From Nearest Refuge (km)
Ailaoshan	China	6	1931	24.17			5.0	15.3	11.0	No	No	248
Bach Ma	Vietnam	7	3500	16.21					22.0	No	No	146
Ben En	Vietnam	8	1790	19.59					23.3	No	No	187
Damingshan	China	2	3000	23.45					21.0	No	No	554
Daweishan	China	6	2000	22.85						No	No	71
Dayaoshan	China	3	1824	24.11			8.3	23.9	17.0	No	No	748
Huanglianshan	China	7	2019	22.77			11.4	19.8	16.6	No	No	79
Jiulianshan	China	2	2155	24.56					16.4	No	No	1182
Khao Ang Ru Nai	Thailand	5	1342	13.23						No	No	266
Khao Yai	Thailand	4	2326	14.17	5		18.7	28.3		No	No	242
Mangshan	China	2	1800	24.97					17.2	No	No	1032
Nam Et Phou Louy	Laos	3	1600	20.48						No	No	244
Nam Kading	Laos	10		18.41						No	No	132
Nanling	China	3	1705	24.82			9.0	26.0	17.7	No	No	1039
Neilingding-Futian	China	1	1948	22.42					22.0	No	No	992
Nonggang	China	5	1350	22.37	7				22.0	No	No	418
Phong Nha-ke Bang	Vietnam	9	2030.5	17.58					24.1	No	No	34
Pu Mat	Vietnam	9	1529.5	18.95			1.7	42.6	23.5	No	No	137
Shiwandashan	China	3	2000	21.87			18.8	26.3	21.8	No	No	507
Xishuangbanna	China	7	1900	21.88	7		15.1	21.7	21.7	No	No	138
Cat Tien	Vietnam	9	2575	11.44			24.0	29.0	25.4	No	Yes	
Doi Inthanon	Thailand	5	1907.5	18.52	6		16.1	25.7		No	Yes	
Dong Ampham	Laos	6		14.95						No	Yes	
Hin Namno	Laos	12	2000	17.42						No	Yes	
Huai Kha Khaeng	Thailand	9	1476	15.39	6		17.7	30.4		No	Yes	
Jinpingfenshuiling	China	7	2303	22.69					17.7	No	Yes	
Kaeng Krachan	Thailand	7	1300	12.89						No	Yes	
Nakai-Nam Thuen	Laos	8	2750	17.91						No	Yes	
Nam Ha	Laos	6	1500	20.93						No	Yes	
Phu Khieo	Thailand	7	1377	16.33	4		15.8	27.9	21.5	No	Yes	
Thung Yai Nareusan	Thailand	9	1560.5	15.33	4		18.3	30.7		No	Yes	
Xe Pian	Laos	4	1750	14.48						No	Yes	
Gunung Palung	Indonesia	8	4500	1.24					32.0	Yes	No	469
Kemasul	Malaysia	7	1546	3.77		879	27.0	33.0		Yes	No	1025
Krau	Malaysia	7	2120	3.72	1	371				Yes	No	1019
Kutai	Indonesia	8	2177	0.37	1					Yes	No	351
Lesong	Malaysia	6	2500	2.73		485				Yes	No	1202
Sungai Lalang	Malaysia	5	2554	3.50		538				Yes	No	893
Sungai Tekam	Malaysia	6	2207	4.17	1	547				Yes	No	1034
Tanjung Puting	Indonesia	7	2400	2.94	0	857				Yes	No	436
Barito Ulu	Indonesia	8	4386	0.38	1					Yes	Yes	
Bukit Barisan Selatan	Indonesia	8	3000	5.23						Yes	Yes	
Danum Valley	Malaysia	8	2822	4.94						Yes	Yes	
Gunung Lueser	Indonesia	7	2729	3.57	1	475				Yes	Yes	
Mount Kinabalu	Malaysia	7	2392	6.03	0		15.4	35.4	24.3	Yes	Yes	

Table 1.2. Pearson's correlations between species richness and ecological variables.

Variable	N	R	p
Rainfall	44	0.17	ns
Latitude	45	-0.39	$p<0.05$
Dry Months	11	-0.27	ns
Tree Density	7	0.29	ns
Mean Minimum Temperature	15	0.16	ns
Mean Maximum Temperature	15	0.42	ns
Mean Temperature	20	0.45	$p<0.05$

Table 1.3. General Linear Model Results.

General Linear Model I		
Variable	F-Value	p
Intercept	20.13	$p<0.05$
Rainfall	0.26	ns
Island/Continent	0.73	ns
Refuge/Non-Refuge	5.43	$p<0.05$

General Linear Model II		
Variable	F-Value	p
Intercept	146.38	$p<0.05$
Distance from Equator	6.18	$p<0.05$
Refuge/Non-Refuge	5.96	$p<0.05$

Fig. 1.1. Map of protected areas included in this analysis.

Fig. 1.2. Pearson's correlation between species richness and distance from the equator ($r= -0.39$, $p<0.05$).

Fig. 1.3. Lowess localized regression for species richness as a function of mean annual rainfall.

Fig. 1.4. Box plot for the difference in species richness between island and mainland sites ($t= -1.42$, $p= 0.16$).

Fig. 1.5. Box plot for the difference in species richness between refuge and non-refuge sites ($t= -2.76$, $p<0.05$).

Fig. 1.6. Pearson's correlation between species richness and great circle distance from the nearest refuge for non-refuge sites ($r= -0.51$, $p<0.05$).

Fig. 1.7. General Linear Model II. Pearson's correlation for non-refuges ($r= -0.44$, $p<0.05$) and refuges ($r= -0.10$, $p=0.70$).
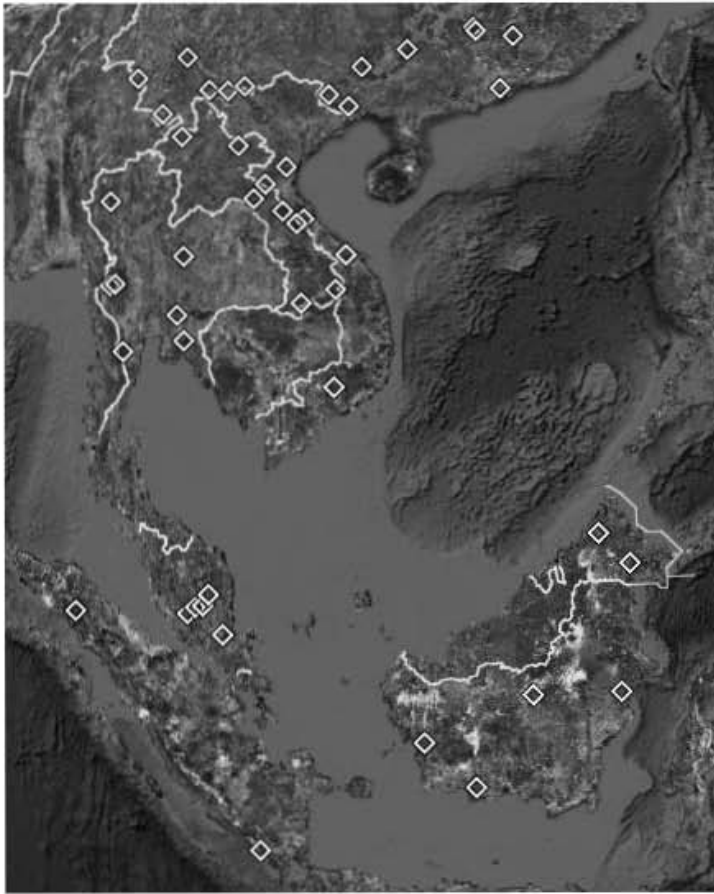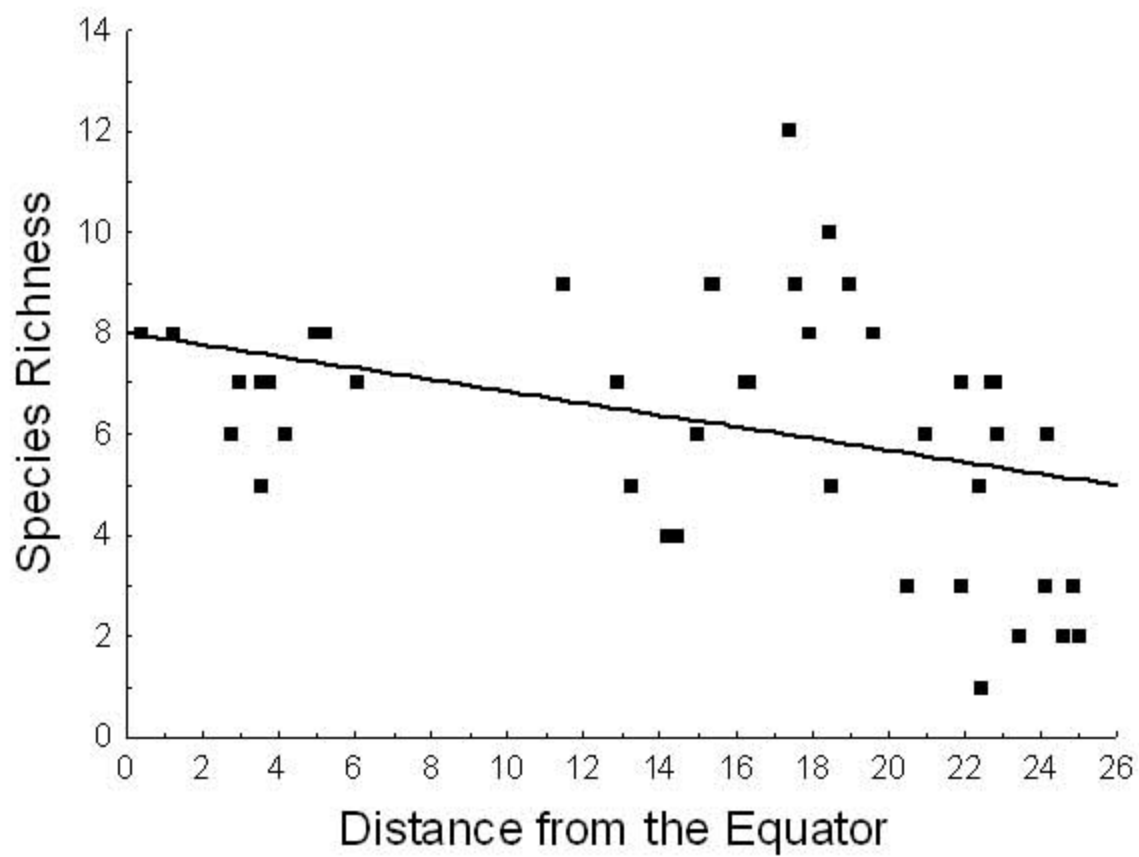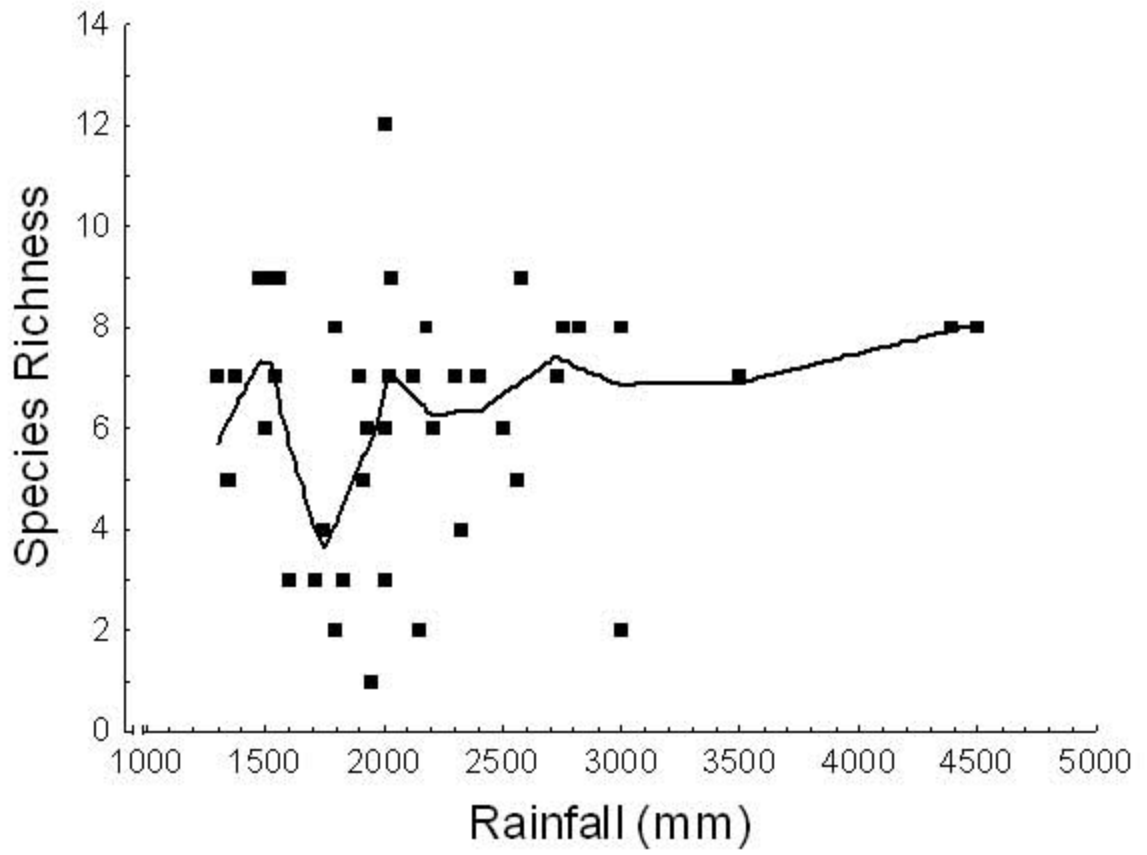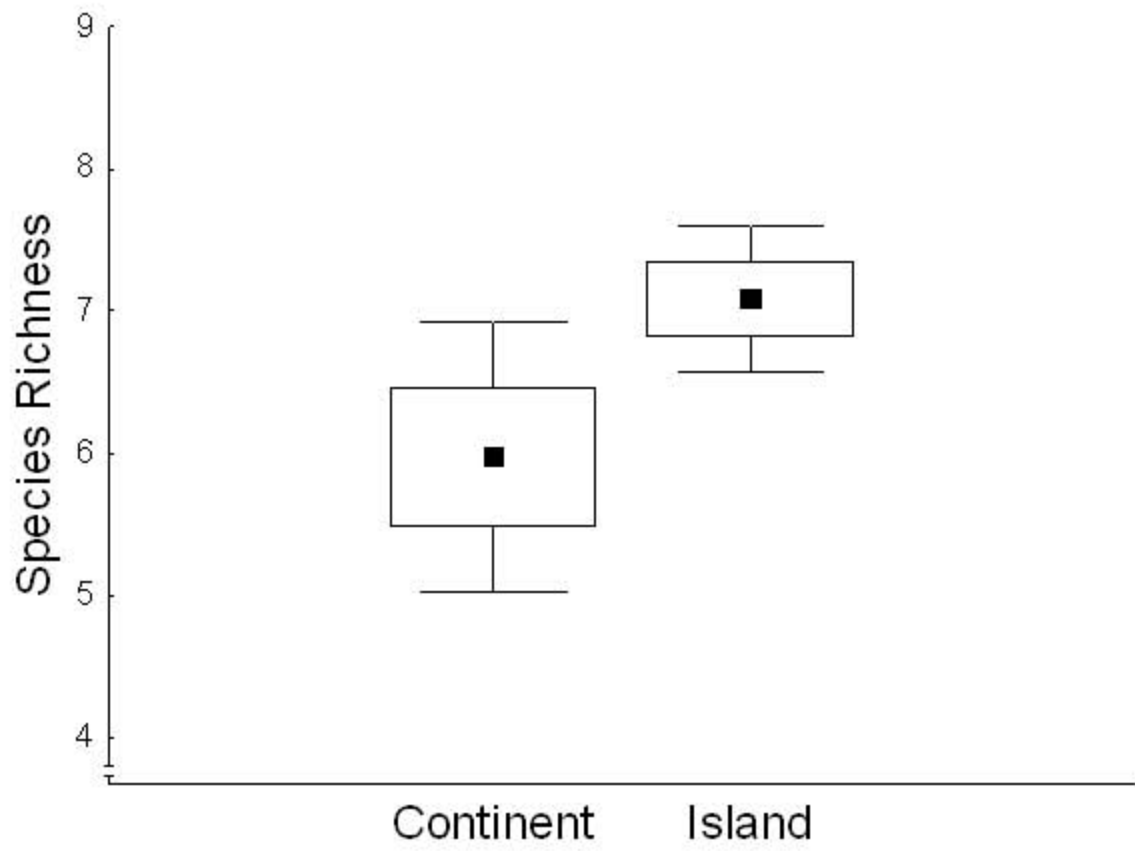
Fig 1.1.

Fig 1.2.

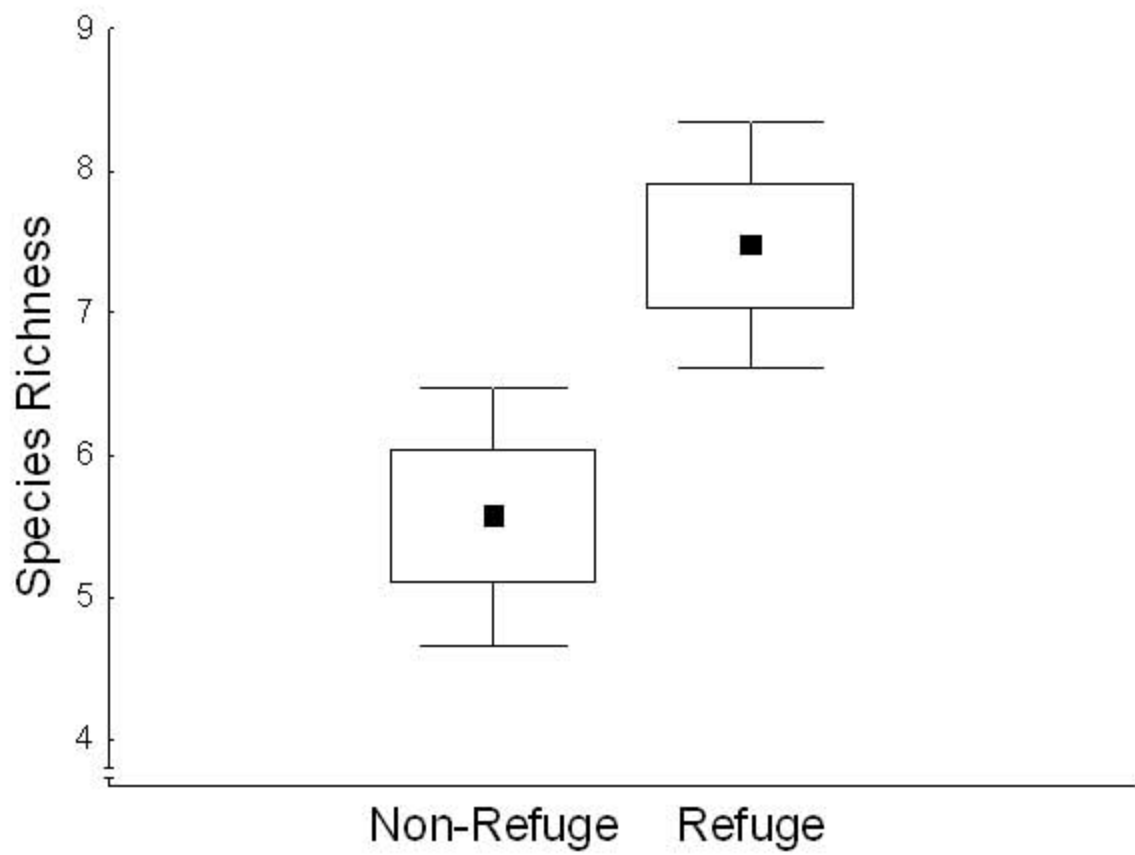**Fig 1.3.**

Fig 1.4.

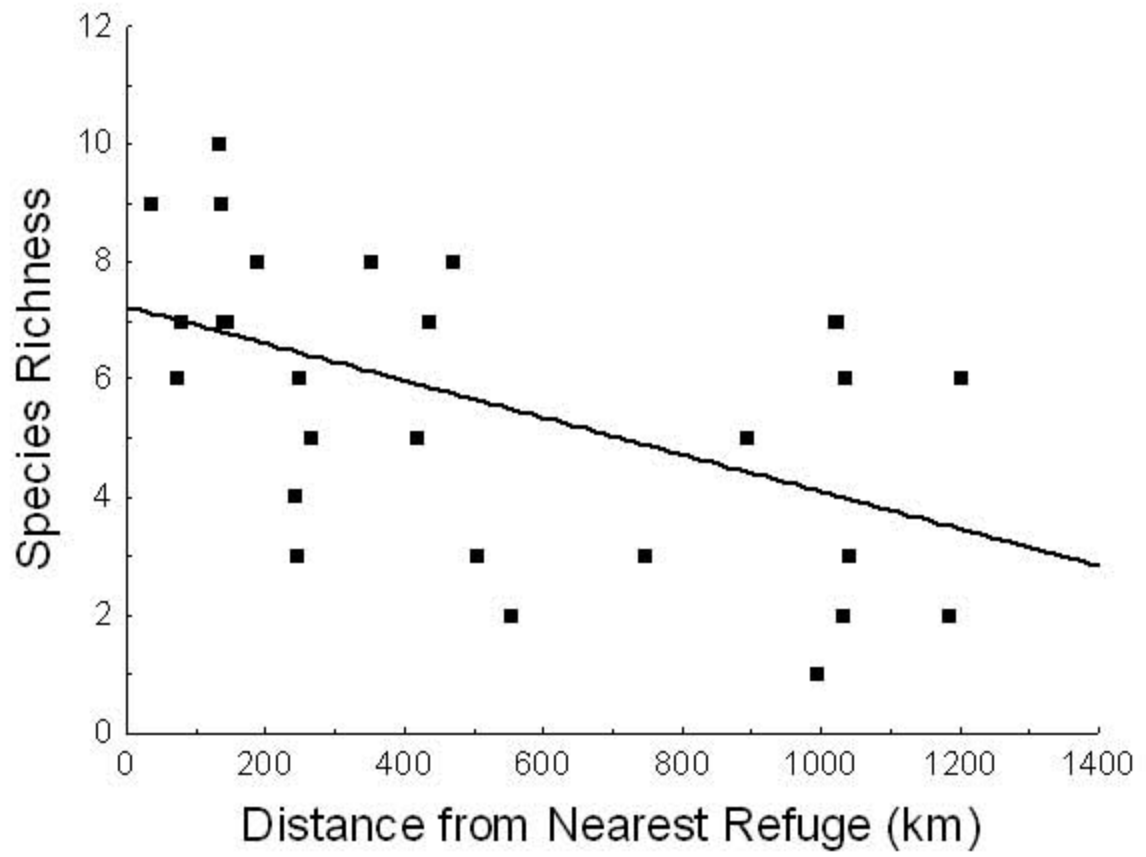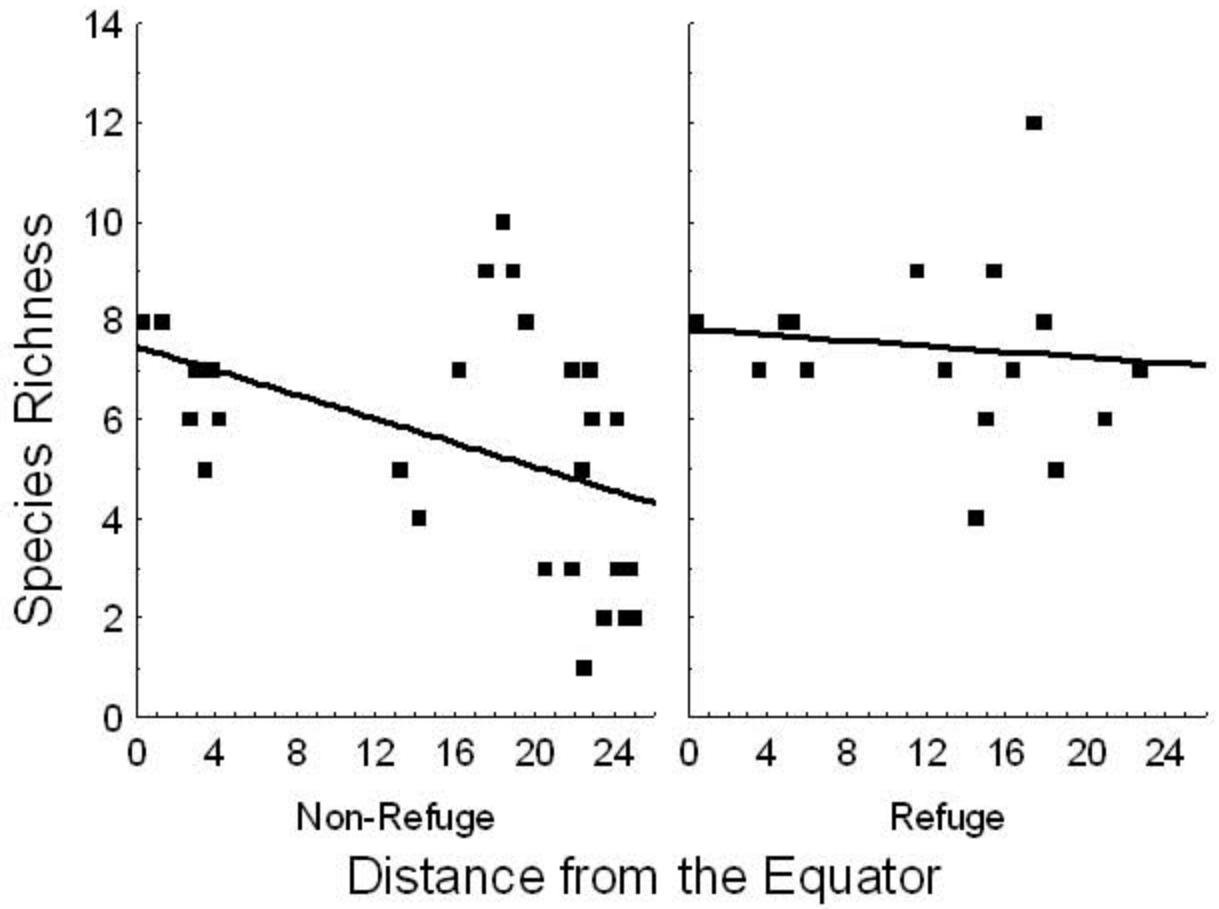**Fig 1.5.**

Fig 1.6.

Fig 1.7.

How Reliable are Density Estimates for Diurnal Primates?

Abstract:

      Primate population assessments provide the basis for comparative studies and are necessary prerequisites in determining conservation status. The most widely used assessment method is line transect sampling which generates systematic data fast and comparatively cheaply. In contrast, the presumably most reliable method is long-term monitoring of known groups, which is both slow and costly. In order to assess the reliability of various analysis methods, we compared group and population densities for white-handed gibbons (*Hylobates lar carpenteri*) and Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) derived from transect walks with those from long-term group follows at Phu Khieo Wildlife Sanctuary, Thailand. A 4-km transect was walked regularly over 30 months (480 km total), resulting in 155 gibbon sightings and 125 leaf monkey sightings. Densities were then estimated using (1) the program DISTANCE, and (2) the Kelker method based on (2.1) perpendicular distances (PD) or (2.2) animal-to-observer distances (AOD). These three estimates were compared to values based on known home ranges, accounting for home range overlap (95% Kernels), combined with group size data. Analyses of line transect data consistently overestimated group densities for both species, while underestimating group size for leaf monkeys. Quality of results varied according to each species group size and spread. However, this study, in accordance with previous studies, found that values derived using AOD (or derivations of this method) matched most closely with population estimates based on home range data.

Introduction:

      Primate population assessments provide valuable data for both comparative and conservation studies. With 114 species of primates listed as critically endangered, endangered, or vulnerable on the IUCN Red List (IUCN 2006), and with many others also experiencing threats such as disease, poaching, and habitat loss, there is an urgent need for successful management strategies. In developing such strategies, it is essential to have reliable baseline density estimates, as well as assessments of changes in density through time, in combination with evaluations of the importance of different habitats for primate conservation (Plumptre and Reynolds 1994). At the same time, population assessments are also pivotal in comparative studies that investigate primate density in relation to a number of factors, such as habitat quality and structure (Peres 1997), food availability (Worman and Chapman 2006), geography and climate (Harcourt 2006), and behavior (Butynski 1990).

      Two primary methods are employed in population assessments. The first, long-term monitoring of home range size and overlap in conjunction with group size data, is time and money intensive (NRC 1981). However, it is believed to be the most reliable, and densities calculated from this type of data are sometimes even considered absolute measures (Brugiere and Fleury 2000). The second, line-transect surveying, is more efficient in terms of both time and finances (NRC 1981), and for this reason is commonly used (Haugaasen and Peres 2005; Rovero *et al.* 2006; Teelen 2007; Weghorst 2007).

Several assumptions must be met when using line-transect sampling, including: that no animals on the transect line are missed, animals do not move before they are detected, animals are not counted twice, distances and angles are measured accurately, and sightings are independent events (White and Edwards 2000; Buckland *et al.* 2001; Ross and Reeve 2003). Failing to meet any of these assumptions may affect the reliability of results (Buckland *et al.* 2001). It is, however, often not clear what assumptions have been violated, or how these violations, if known, affect density estimates.

Several methods of analyzing line transect data to determine density and group size have been suggested (NRC 1981; Brockelman and Ali 1987; Whitesides *et al.* 1988; Buckland *et al.* 2001); yet, there remains debate over which method is most reliable (Brugiere and Fleury 2000; Fashing and Cords 2000; Plumptre and Cox 2006). Distance sampling (via the software package DISTANCE 5.0), determines a detection function for the probability of seeing an animal at various perpendicular distances from a transect. Groups that are close to the line are more likely to be detected than those far from the line (affecting density estimates), and an observer is more likely to see all members of a group that is closer than further (affecting group size estimates). DISTANCE is designed to correct for these biases (Buckland *et al.* 2001). However, this program requires a large number of sightings (n>40) per species, so that comparisons of primate line transect analysis methods have often been unable to test its effectiveness (Brugiere and Fleury 2000). For other analytical methods, it is necessary to determine the effective distance at which individuals and/or groups are detected with 100% probability. There are two methods for determining this effective distance, the Kelker method based on either perpendicular distance (PD) or based on animal-to-observer distance (AOD). Either distances between the animal and observer or perpendicular distances between the animal and the transect line are used to determine the effective distance. For both, the drop in detection probability is found post-hoc (via histograms with different distance classifications (NRC 1981)). Data derived from PD analyses have repeatedly been found to overestimate primate densities (Defler and Pintor 1985; Fashing and Cords 2000). On the other hand, data derived from AOD analyses often closely match absolute measures of primate densities (Chapman *et al.* 1988; Fashing and Cords 2000). However, because the AOD method has no theoretical basis and lacks a mathematical framework, some caution against its use (Plumptre and Reynolds 1994).

In this study, we compare measures of group density, individual density, and group size for the two most common primate species (*Hylobates lar carpenteri* and *Trachypithecus phayrei crepusculus*) in a dry evergreen forest in Thailand. With the aim of determining the most accurate method of analyzing line transect data, we compare the results of line-transect surveys to absolute measures of density and group size.

Methods:

Study Site

Data were collected at Huai Mai Sot Yai study site (16°27'N, 101°38'E, elevation 600-800 m) in the Phu Khieo Wildlife Sanctuary, northeastern Thailand. The site comprises 3,000-4,000 ha of hill and dry evergreen forest with patches of dry dipterocarp forest. The diurnal primate community at the site consists of six species, listed here in descending order of abundance: Phayre's leaf monkeys (*Trachypithecus phayrei*

crepusculus), white-handed gibbons (*Hylobates lar carpenteri*), Assamese macaques (*Macaca assamensis*), northern pig-tailed macaques (*Macaca leonina*), and rhesus macaques (*Macaca mulatta*) (Borries *et al.* 2002). Stump-tailed macaques (*Macaca arctoides*) have been encountered as well, but are extremely rare. One nocturnal species, the northern slow loris (*Nyctocebus bengalensis*) is also present at the study site (Kumsuk *et al.* 1999). Here we report data for the two most common diurnal primate species, white-handed gibbons and Phayre's leaf monkeys.

Data Collection
Home Range and Overlap:
    For white-handed gibbons, home range data were collected from one habituated group (called G1) which was observed from November 2003 until October 2004, for two to four days each month. During this time G1 consisted of 3 to 5 members (average 3.75; Umponjan, 2006). G1 was followed from dawn to dusk, with GPS points (Garmin® GPS 12 or 12 XL) taken at the approximate center of the group every half and full hour, and at the first and last contact (resulting in 139 GPS points). In addition, whenever G1 encountered one of its four neighboring groups, the location of the intergroup encounter was recorded and the group size and composition of the neighboring group was noted.
    Density data for Phayre's leaf monkeys were derived from data collected from March 2004 to June 2006 on habituated study groups. Here, we primarily focus on one of these groups (PA). With a size of 17.3 individuals on average (range 14-20) PA represents a medium sized group compared to the population mean of 16.3; range 3-33 (; Koenig *et al.* 2004; Gibson and Koenig submitted). One of the other focal groups (PS, 12.1 individuals, range 9-16) is a neighbor to PA allowing assessment of overlap in home ranges.
    GPS points were taken for Phayre's leaf monkeys at the approximate center of the group every half and full hour, and at the first and last contact (PA: 311 days; PS: 162 days). In addition, whenever PA met one of its four neighbors (including PS), the location of the intergroup encounter was recorded. Although data on the size and composition of neighboring non-focal groups were collected during these encounters, they were almost always incomplete. For this analysis we relied on population surveys of non-focal groups, which were conducted two to four times a year because they provided better group size estimates.
    For both species, solitary individuals were encountered, but very infrequently. While we know from these rare encounters that solitary animals exist, corresponding density data must be considered subject to chance and very unreliable. Consequently solitary white-handed gibbons and Phayre's leaf monkeys were not included in density calculations based on home ranges.

Transect:
    A transect was established at Huai Mai Sot Yai on November 07, 2000. It was placed in dry evergreen forest, such that it was at least one kilometer away from the sanctuary road at all points, but as close as possible to habituated primate groups. The transect originated at Universal Transmercator coordinates (UTM; zone 47Q) 778000/1820000. It ran for 4 km (Peres 1999), in an angle of about 45° until approximately UTM 780730/1822900.

Data were collected over four transect walks per month from December 2000 to September 2001 and from February 2002 to September 2003 (for a total of 30 months, 480 km walked total during 120 walks). A sub-sample of the data from these transect walks (December 2000 through September 2001) were used in a previous study (Borries *et al.* 2002). Usually the transect was walked on four consecutive days in the middle of the month. Walks began at first daylight, if not prevented by wind, rainfall, fog, or the presence of large mammals (e.g., elephants). Typically we started around 0700 h (range 0545-0805 h) and reached the end of the transect around 1145 h (range (1000-1335 h), resulting in a mean duration of 4.42 h (range 4.09-7.25 h) on the transect, which included all contact times and times out (see below). We moved as quietly as possible and monitored velocity by means of a stopwatch (3 min per 50 m, mean 1.00km/h, range 0.96-1.02). While on the transect, we tried not to move backwards and did not leave it (Peres 1999).

During walks, our attention was directed forward and to either side, scanning from the canopy to the ground. However, 14% of the 354 primate sightings occurred only after we had already passed the animals. These encounters were included in the analysis. If an animal was heard or seen, we stopped and remained for 9.4 min on average (range 0-23 min), usually staying no longer than 10 minutes. If at least one individual was actually seen, the encounter was rated as a primate contact. For instance, gibbons identified and located via singing only were not included. The mean number of primate sightings was 3.0 (range 0-8) per walk. We took time out and stopped during transect walks (mean 13 min per walk, range 0-158): (i) if large or potentially dangerous animals had to be avoided or (ii) if rain, fog, or wind prevented reliable detection of animals.

For each contact with primates, the following data were noted (NRC 1981; Brockelman and Ali 1987; Krebs 1999; Peres 1999): species, mode of detection (visual or auditory), time when contact started, and the location on the transect. Attempts were also made to assess the center of the group, its distance, compass bearing, and group spread. However, group spread usually was not circular, the group center was often unidentifiable, and observers were unable to agree on its location. As a result, a previously suggested analysis method that incorporates group spread (Whitesides *et al.* 1988) was not included in this study. Instead, for the first individual sighted we noted: the animal-to-observer distance and compass bearing (together used to calculate perpendicular distance), height, and activity at the time of detection. We counted all individuals (i.e., all animals seen plus movements or sounds heard simultaneously at other locations) to conservatively estimate the number of additional individuals present. This resulted in a minimum number of individuals (i.e., all individuals seen, see above) and a maximum number of individuals (i.e., the minimum number plus the highest number of additional individuals estimated). Here we report results for the maximum number of individuals only. Whenever possible, distances were measured by means of an optical rangefinder (accuracy ±1 m). Otherwise, distances and heights were estimated to the nearest meter. Distance estimates were calibrated monthly, as was the inter-observer reliability for all other measures taken. Twenty-three percent of the walks were performed by a single observer, while the other 77% were performed by two observers. No difference in detection probability existed in relation to the number of observers (Borries *et al.* 2002).

Data Analysis
Home Range and Overlap:

GPS data for white-handed gibbons were analyzed using the program Mapsource 5.4 creating 95% kernels (Worton 1989) to describe the home range (59.7 ha). Because only one group was followed, we used the data from intergroup encounters to assess the home range overlap. This resulted in an exclusive area of 41.0 ha for G1 with the remaining 18.7 ha shared with neighboring groups (Umponjan 2006).

For the density analysis of Phayre's leaf monkeys, we discarded all GPS values with errors greater than 10 m. In total, we recorded 4,537 points from PA and 3,235 points from PS (Gibson and Koenig submitted). GPS data were then mapped in ArcView 3.2 and we used the Animal Movement extension (Hooge and Eichenlaub 1999) to create 95% kernels to describe the home ranges (Worton, 1989; PA: 102.5 ha, PS: 52.2 ha). We then mapped and measured the overlap of groups PA and PS in ArcView 3.2 (3.0 ha representing 2.9 and 5.8% of their total home ranges) and determined the length of their joint border. Next we determined the length of joint borders to all other neighbors and extrapolated the overlap area with neighboring groups accordingly (based on PA-PS overlap).

For both species, we used the information of exclusive and shared range use together with information of the size of the groups to calculate group and population density data. Following NRC (1981), we first calculated group and population density for exclusively used areas and added parts of the home ranges that were used by more than one group apportioned by the number of groups or their size.

Transect:

Primate density and group size measures were calculated from transect data for white-handed gibbons and Phayre's leaf monkeys separately, using the (1) program DISTANCE 5.0 (http://www.ruwpa.st-and.ac.uk/distance), and the (2) Kelker method based on (2.1) perpendicular distances (PD) and (2.2) animal-to-observer (AOD) distances.

1) In the program DISTANCE, the conventional distance sampling function of the program was used (Buckland *et al.* 2001) to independently estimate group density and group size for each species. Four candidate models were tested in the program for fit to the distribution of transect data, including the uniform key with cosine polynomial expansion, uniform key with simple polynomial expansion, half-normal key with hermite polynomial expansion, and hazard-rate key with the cosine polynomial expansion. For each species, the probability of detection function with the lowest Akaike's Information Criterion (AIC) value was chosen separately for groups and for solitary animals (Buckland *et al.* 2001).

DISTANCE analysis produced results for group density and bias-corrected group size. Individual density was then calculated manually, by multiplying corrected mean group size by group density to obtain two values (solitary individuals/km^2 and group individuals/km^2).

2) For both Kelker based methods, group and population densities were assessed using the equation:

$$D = n / 2 L a$$

where D = density of animals or groups per unit area, n = number of animals or groups seen along the transect, L = total length of the transect, and a = half the effective strip width.

The factor a is a location and species-specific cut off point which determines the area around the transect where the detection probability is assumed to be one (NRC 1981). In our analysis, all sightings up to the cut-off point were included in the analysis, but sightings beyond the cut-off point were excluded. (2.1) In order to determine the effective strip width for perpendicular distance calculations, the distribution of perpendicular distances was analyzed separately (in blocks several meters wide) for each species to find the detection cut-off points. (2.2) The same procedure was used to find the cut-off point for the AOD distributions, using animal-to-observer distance data. For example, a cut-off point at 30 resulted in a transect width of 2 x 30m. Together with a total transect length (L) of 480 km, an overall area of 28.8 km^2 was covered during 120 walks for this particular species.

For each Kelker based method (PD and AOD), transect data were analyzed, using the equation above, to determine group density (groups/km^2), solitary animal density (individuals/km^2), and density of group living animals (individuals/km^2). Mean group size was determined based on all groups detected within the effective strip.

We determined the deviation of results from each transect analysis method from the results of home range analysis, using the following equation:

$$d = (t - h / h) \times 100$$

where d = deviation between methods, t = transect result of interest, and h = home range result for a particular species.

Results:

A total of 155 white-handed gibbon sightings and 125 Phayre's leaf monkey sightings were recorded over the course of all transect walks. All other primate sightings ($n = 62$) were of macaques; for each macaque species data were too limited to complete analyses.

Detection Probabilities

Density estimates from DISTANCE were based on the detection probability function with the lowest AIC values. For solitary white-handed gibbons, a uniform detection function with first order cosine adjustment had the best fit. The half-normal detection function was the best fit for gibbon groups (Figure 2.1a). For solitary Phayre's leaf monkeys, DISTANCE results indicate that detection probability was 1.0 for all distances at which solitary leaf monkeys were observed. For leaf monkey groups, the uniform detection function with second and fourth order polynomial expansions provided the best fit to data (Figure 2.1b).

Density estimates using the Kelker method were based on primates observed within effective strips, which were determined based on the distribution of detection distances shown in Figure 2.2. The effective strip width for white-handed gibbons was 26 m for PD and 55 m for AOD. For Phayre's leaf monkeys, the effective strip width was 34 m for PD and 35 m for AOD.

Primate Densities and Group Sizes

      White-handed gibbon density and group size results are presented in Table 2.1. Data from home range size and overlap indicated a group density of 2.0 groups/km^2. All transect based analysis methods estimated larger group densities (Figure 2.3). The DISTANCE method estimated 3.3 groups/km^2 (65% larger). The Kelker based methods estimated 3.0 groups/km^2 (50% larger) based on perpendicular distances and 2.3 groups/km^2 (15% larger) based on animal to observer distances.

      Demographic data from habituated groups indicated a mean group size of 3.2 individuals/group for gibbons. Estimates of mean group size exceeded this value for all transect based analysis methods (Figure 2.3), with a mean group size of 3.7 individuals/group (16% larger), 3.7 individuals/group (16% larger), and 3.5 individuals/group (9% larger) recorded using the DISTANCE, PD based Kelker method, and AOD based Kelker method, respectively.

      Based on home range and overlap data, white-handed gibbon population density was approximately 8 individuals/km^2 at Huai Mai Sot Yai. The DISTANCE and PD based estimates of population density exceeded this value (Figure 2.3). The DISTANCE program estimated a population density of 12.2 animals/km^2 (53% larger); the PD based Kelker method estimated 11.3 animals/km^2 (41% larger). The AOD based analysis method estimated population density to be lower 1% lower (Figure 2.3), estimating 7.9 animals/km^2. For each measure (group density, mean group size, and population density), AOD based Kelker method provided results that were closest to those estimated using the home range and demographic data (Figure 2.3).

      Phayre's leaf monkey density and group size results are presented in Table 2.2. Home range size and overlap data indicated a group density of approximately 1.1 groups/km^2. Transect based methods estimated group density to be between 91 and 209%larger (Figure 2.4). DISTANCE estimated 3.4 groups/km^2, the perpendicular based Kelker method estimated 2.9 groups/km^2, and AOD based Kelker method estimated 2.1 groups/km^2.

      Demographic data from habituated Phayre's leaf monkeys indicated a mean group size of approximately 16 individuals/group. In comparison, transect based data estimated group sizes to be smaller (Figure 2.4). DISTANCE estimated a mean group size of 9.3 individuals/group (42% smaller), PD based Kelker method estimated 9.2 individuals/group (43% smaller), and AOD based Kelker method estimated 8.6 individuals/group (46% smaller).

      Home range based data estimated population density of 20.2 individuals/km^2. DISTANCE and PD based analysis methods both exceeded this value, estimating 31.6 indviduals/km^2 (56% larger) and 26.3 individuals/km^2 (30% larger), respectively. The estimate of Phayre's leaf monkey population density based on AOD Kelker method, on the other hand, was lower than that estimated from home range data, with 18.0 individuals/km^2 (11% smaller). For two out of the three measures reported (namely group density and population density) estimates based on AOD methods were most comparable to estimates based on home range and demographic data.

Discussion:

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For both white-handed gibbons and Phayre's leaf monkeys, the AOD analysis method provided the most accurate estimates of group density and population density. DISTANCE, PD, and AOD analyses all provided similar estimates of group size (with the AOD analysis providing the most accurate results for white-handed gibbons).

Transect results that are ≤10% different from home range results are usually considered reliable estimates of population parameters (NRC 1981; Whitesides *et al.* 1988). For gibbons, all AOD results were reasonably close to, or below, this 10% value. However, for Phayre's leaf monkeys, both the group density and group size values are outside the reliable range. Such deviations from expectation may be the result of violating the assumptions of line transect sampling (NRC 1981; Buckland *et al.* 2001). In this case, it is necessary to both determine the assumption that has been violated and attempt to control for it (Buckland *et al.* 2001). For Phayre's leaf monkeys all analysis methods underestimated group size (by 42-46%). In other words, Phayre's leaf monkey groups seen along the transect line are on average roughly 1/2 the size of those seen in long-term investigations of home range and group size. On the other hand, all analysis methods overestimated group density (by 90-209%). The AOD analysis provided the lowest overestimate, which indicated that for each leaf monkey group that is expected to be present, roughly two groups were counted on the transect. The overestimate of group density, combined with the underestimate of group size, counterbalanced each other to lead to reliable estimates of population density, using AOD analysis. Based on our experience, completing long term observations, the most reasonable explanation for this pattern is that leaf monkeys regularly form subgroups that may forage and travel independently for hours or days at a time; these subgroups were likely counted as separate entities along the transect line.

While this study is focused on two particular species of primates, it is important to attempt generalizations that may assist with surveys of all primate species. Though it has been suggested that the AOD analysis method should not be used in line transect analysis because it lacks a mathematical framework (Plumptre and Cox 2006), this study, along with others (NRC 1981; Defler and Pintor 1985; Chapman *et al.* 1988; Struhsaker 1997; Fashing and Cords 2000) has shown that AOD provides the most accurate measures of population parameters from line transect data. However, further customizations of the AOD analysis method may be necessary to account for differences in group spread and group size between different primate species. For species with small group sizes and relatively small group spread (such as the white-handed gibbons in this study), traditional AOD analysis provides reliable results (NRC 1981; Chapman *et al.* 1988; Whitesides *et al.* 1988). For species with larger group size and group spread, data concerning the location of the group center can add accuracy to line transect analysis (Whitesides *et al.* 1988; Fashing and Cords 2000). However, for some species (such as the Phayre's leaf monkeys in this study), a reliable assessment of the location of the group center may not be possible during transect walks, as temporary subgroups may move independently. As a result, if group size estimates are suspected to be incorrect, then group density estimates are also likely to be inaccurate, and only population density assessments may be reliable for use in comparative or conservation work (as the over- and under-estimates of the other two measures counterbalance each other).

Primate line transect surveys are integral to many comparative and conservation projects, both of which may require population parameters to be compared over time and

space. Thus, the usefulness of transect data relies on both accuracy and standardization, so as to ensure that patterns observed are not a byproduct of research design, rather than biological processes. For standardization of primate line transect methods to occur, it is first essential to establish the most accurate means of data collection and analysis. Like others, this study has indicated that the AOD analysis method, with appropriate adjustments, is a good and rather reliable choice for primate surveys.

Table 2.1. Densities of white-handed gibbons derived from transect and home range estimates. *solitary animals not included

Analysis Method	Group Density [Groups/km^2]	Mean Group Size [Individuals/group]	Solitary Animals [Individuals/km^2]	Population Density* [Individuals/km^2]
Home range size and overlap	2.0	3.2	---	8.0
DISTANCE	3.3	3.7	0.6	12.2
Perpendicular Distance	3.0	3.7	0.9	11.3
Animal-Observer Distance	2.3	3.5	0.6	7.9

Table 2.2. Densities of Phayre's leaf monkeys derived from transect and home range estimates. *solitary animals not included

Analysis Method	Group Density [Groups/km^2]	Mean Group Size [Individuals/group]	Solitary Animals [Individuals/ km^2]	Population Density* [Individuals/km^2]
Home range size and overlap	1.1	16.0	---	20.2
DISTANCE	3.4	9.3	0.2	31.6
Perpendicular Distance	2.9	9.2	0.2	26.3
Animal-Observer Distance	2.1	8.6	0.2	18.0

Fig. 2.1. Detection functions from the program DISTANCE for a) white-handed gibbons and b) Phayre's leaf monkeys. Fit functions (half-normal function and uniform function with 2nd and 4th order polynomial expansion, respectively) are represented by the dotted lines (based on maximum number of individual data for all groups).

Fig. 2.2. Effective strip width diagrams using Kelker method for a) white-handed gibbons and for b) Phayre's leaf monkeys. Dotted lines represent the effective strip width within which detection probability is expected to be 1.0 (based on observations of maximum number of individuals' data for all sightings of solitary individuals and groups)

Fig. 2.3. Comparisons of white-handed gibbon density and group size, across different methods, expressed as deviations from the home range based analysis (for details see methods section)

Fig. 2.4. Comparisons of Phayre's leaf monkey density and group size, across different methods, expressed as deviations from the home range based analysis (for details see methods section)
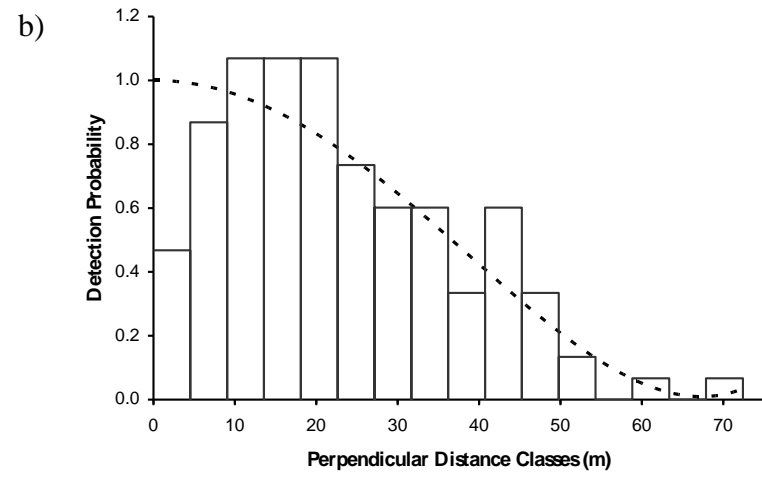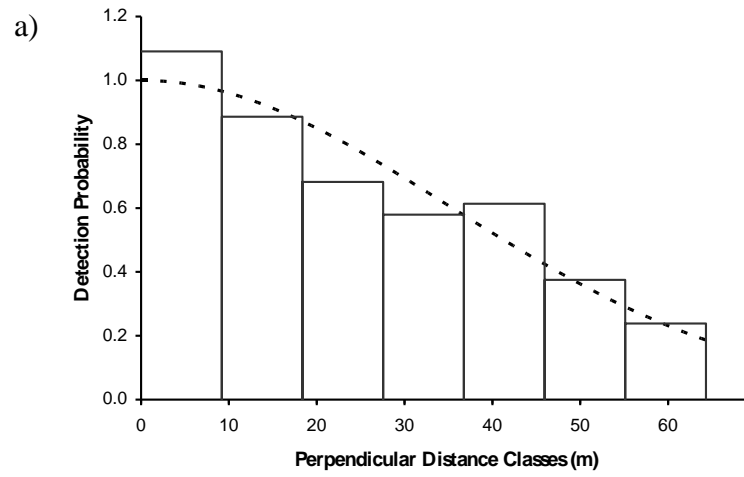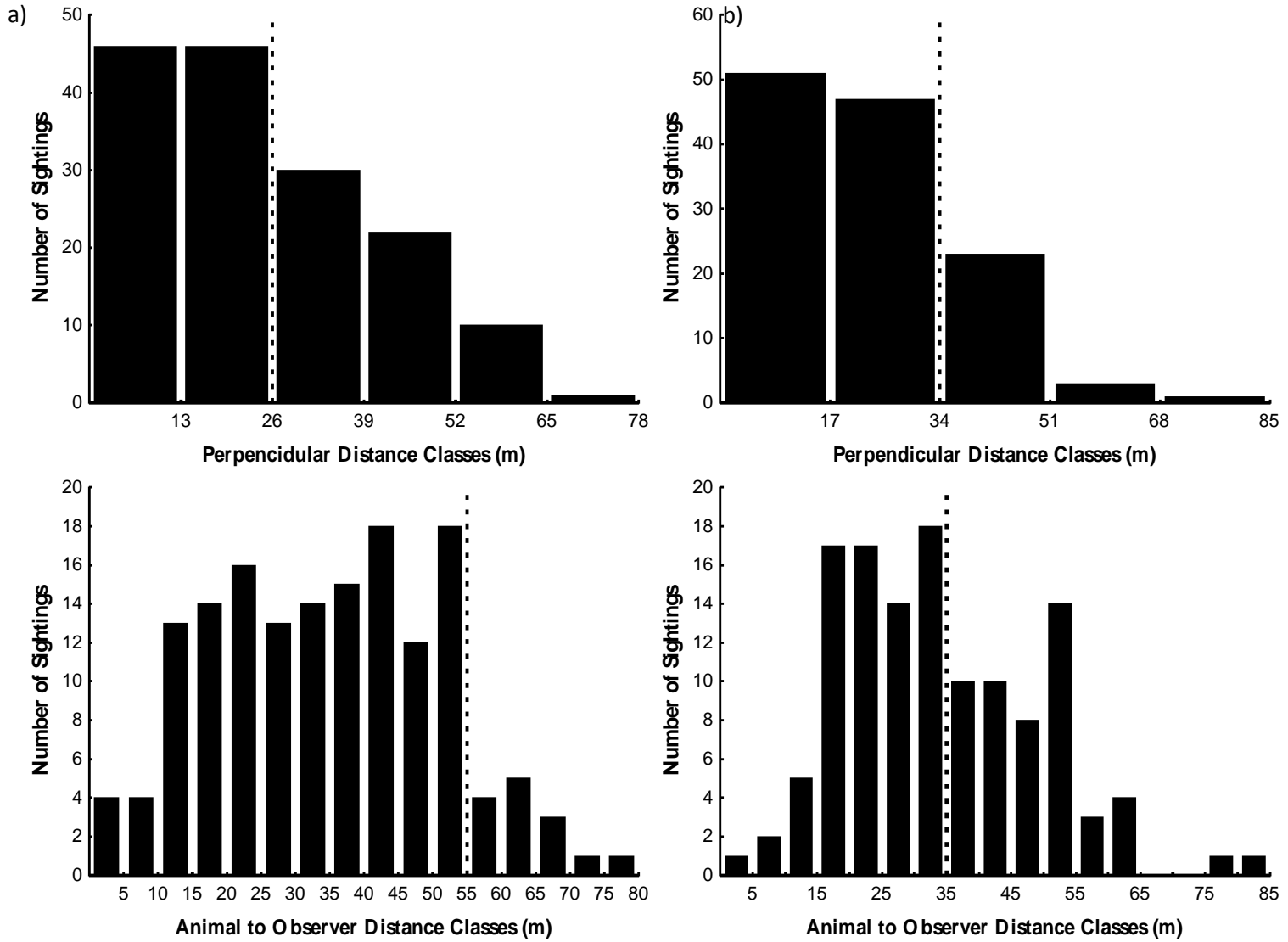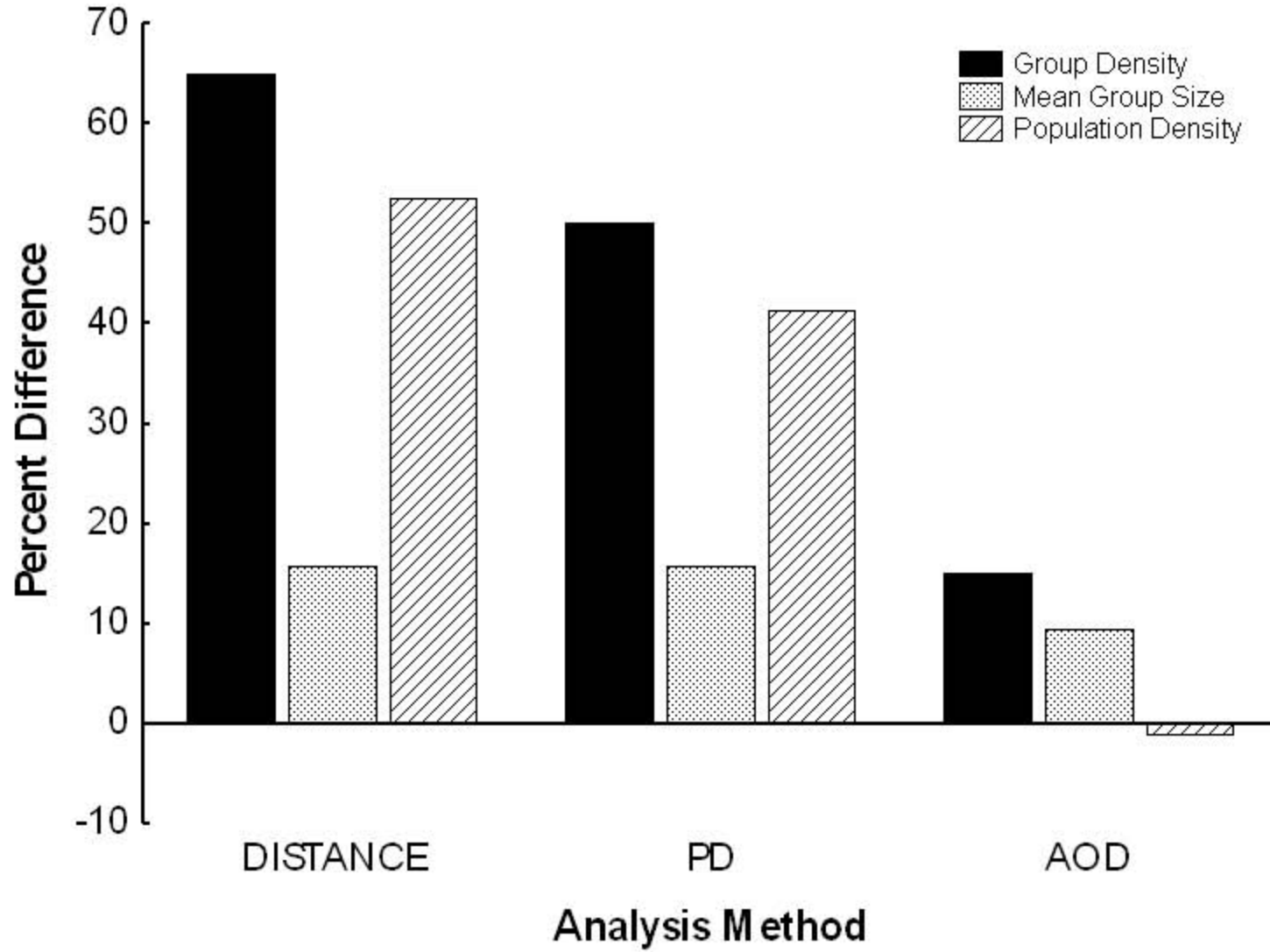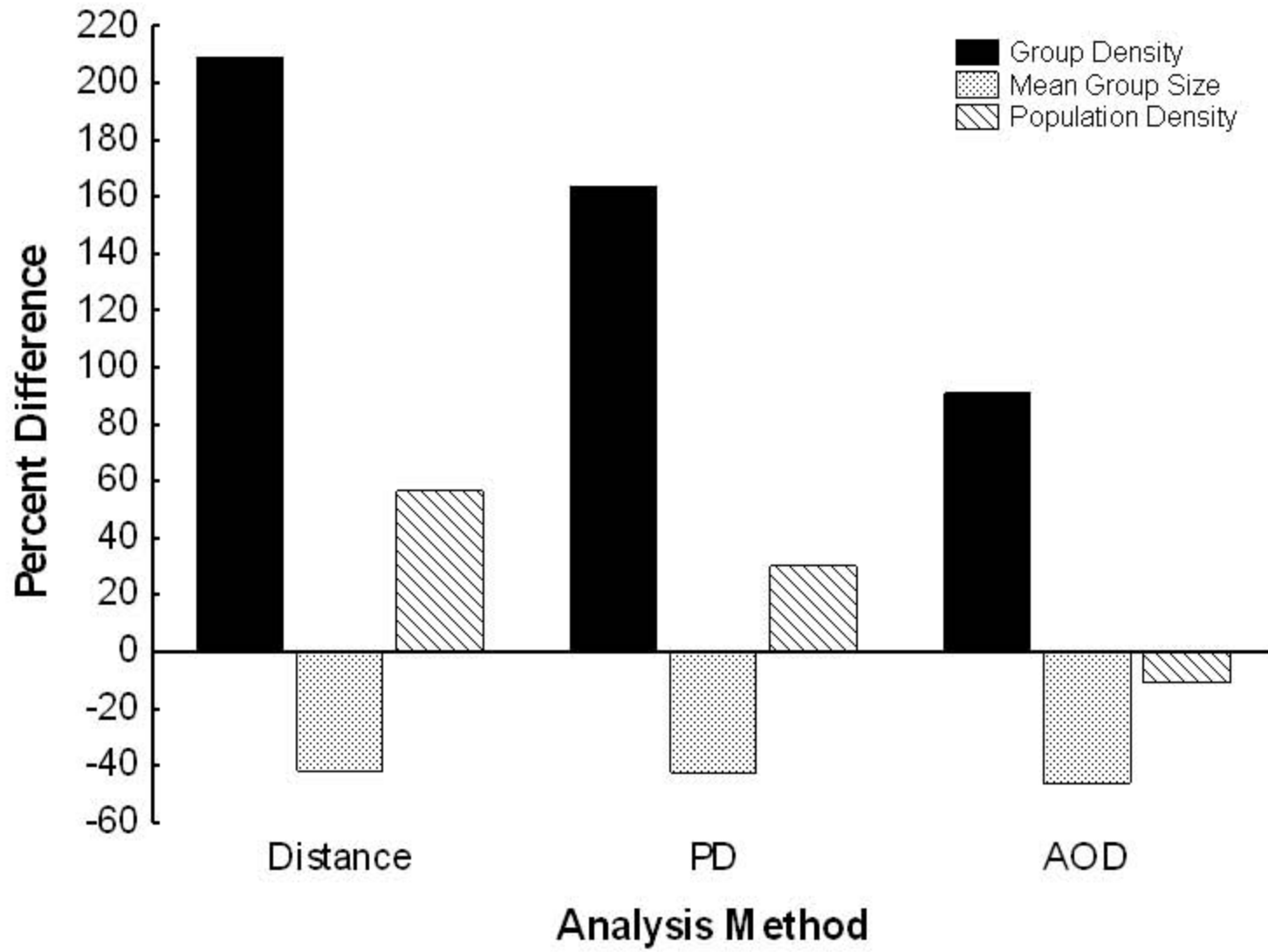
Fig. 2.1.

Fig. 2. 2.

Fig. 2.3.

Fig. 2.4.

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