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## Bed site selection of red muntjac (*Muntiacus muntjak*) and sambar (*Rusa unicolor*) in a tropical seasonal forest

Received: 22 September 2008 / Accepted: 23 March 2009 / Published online: 28 April 2009  
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**Abstract** The selection of bedding sites is important for the ecology of ruminants, but has mainly been described for temperate species. Here we assessed the bed site selection of two Southeast Asian tropical deer, red muntjac and sambar, in Khao Yai National Park, Thailand. We surveyed transects weekly for 10 weeks each in 2003 and 2004 to locate bed sites, and compared the slope, aspect, and forest canopy cover of bed site locations between the two species and with available habitat. As with most temperate deer, muntjac and sambar both avoided sites with low levels of cover for their bed site locations; this could be for concealment or thermoregulation. Sambar also selected flatter sites than would be expected by the availability of topographic slopes; this could be to reduce the energy associated with getting to and from bed sites, or to increase long-range visibility from sites. Muntjac and sambar differed in their choice of aspects for bed sites; muntjac disproportionately chose west-facing areas, while sambar chose east-facing locations. This could represent a strategy by which one species avoids the other, or else differential resource requirements between the two species.

**Keywords** Cervidae · Deer · Habitat selection · Ruminants · Thailand

### Introduction

Ruminants spend much of their time, and derive much of their energy, from ruminating, therefore the choice of locations for bed sites upon which to perform this activity constitutes a critical component of habitat selection for these species (Chen et al. 1999; Germaine et al. 2004; Linnell et al. 2004). Moreover, habitat selection may be very different for bed sites as compared to foraging sites (Mysterud and Ostbye 1995; Teng et al. 2004). Ruminants have a distinct feeding–resting–feeding activity cycle (Cederlund 1989; Jeppesen 1989), and the different phases of the cycle may have different habitat requirements (Mysterud 1996). A body of research has examined bed site selection in temperate ungulates (Mysterud and Ostbye 1995; Mysterud 1996; Chen et al. 1999; Linnell et al. 2004; Jiang et al. 2007), particularly in New World species (Gerlach and Vaughan 1991; Ockenfels and Brooks 1994; Canon and Bryant 1997; Millspaugh et al. 1998; Tull et al. 2001; Germaine et al. 2004). In most of the species studies, bed sites were located in areas of high cover, either to facilitate thermoregulation (Armstrong et al. 1983; Lang and Gates 1985; Mysterud and Ostbye 1995; Millspaugh et al. 1998) or concealment from predators (Alldredge et al. 1991; Linnell et al. 1999; Linnell et al. 2004). Variation in cover and slope of bed site locations can importantly influence the survival rates of individuals (Canon and Bryant 1997).

Very little is known about bed site selection in tropical ungulates. Red muntjac in Hainan Island, China, selected grasslands and thorny scrubland over closed forest for their bed sites (Teng et al. 2004), in contrast to the findings of many temperate ungulates (Millspaugh et al. 1998; Tull et al. 2001; Germaine et al. 2004). Nevertheless, within these broad habitat classes, shrubs for cover and concealment were still critical microhabi-

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tats selected for bed sites (Teng et al. 2004). Thus, an important distinction must be made in the spatial scale of bed site selection; “between-habitat selection” implies differences in, for example, grasslands versus forest (c.f. Hjeljord et al. 1990; Teng et al. 2004), while “within-habitat selection” suggests differences in, for example, cover or small-scale ( $\sim 10$ – $100$  m<sup>2</sup>) topography within a single habitat such as forest (c.f. Smith et al. 1986; Sargeant et al. 1994; Mysterud 1996). Certain studies can address habitat selection across multiple scales, e.g., by concurrently assessing animal use between grasslands and multiple types of forest (Mysterud 1996; Teng et al. 2004).

Moreover, much of the existing research on ruminant bed site selection has examined species that lack sympatric competitors (Lang and Gates 1985; Gerlach and Vaughan 1991; Tull et al. 2001; Germaine et al. 2004). Yet in systems where several ruminants co-exist, the presence of potential competitors may affect the location of bed sites, particularly for smaller or subordinate species. In northeastern China, for example, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) selected different within-habitat conditions for their bed sites (Chen et al. 1999), though this could represent either the effects of competition or differential energy requirements (Chen et al. 1999).

Here we assess the within-habitat selection of bed sites in two sympatric deer species, red muntjac (*Muntiacus muntjak*) and sambar (*Rusa unicolor*; synonym: *Cervus unicolor*), in a tropical seasonal forest in Thailand. These are the two most widespread deer species in tropical Asia (Corbet and Hill 1992), yet information on their bed site selection is extremely scant. Locations of red muntjac bed sites at the between-habitat scale have been assessed in the grasslands, savannahs, and mixed forests of Hainan Island (Teng et al. 2004), but never in the forests of mainland Asia. To our knowledge, the bed site selection of sambar has not been examined at all. We determined bed site locations using transects for field sign (regurgitated seeds and body imprints) and assessed habitat factors (canopy cover, slope, and aspect) at each site.

## Methods

### Study site and species

We performed this study in Khao Yai National Park in northeastern Thailand. Khao Yai (14°26'N, 101°22'E) has an area of 2,168 km<sup>2</sup> and is primarily composed of seasonal moist evergreen forest (Smitinand 1977). Elevation ranges from approximately 700 to 900 m, and average annual rainfall is approximately 2,200 mm, mostly falling from May to October; a pronounced dry season occurs from November to April. We worked on a 30 ha forest dynamics plot in the Mo Singto area of the central western portion of Khao Yai. The plot was surveyed

in 2004–2005 and all trees and shrubs over 1 cm DBH were tagged, mapped and identified; there are  $\sim 270$  tree and shrub species  $\geq 1$  cm DBH on the plot. Most of the plot contains seasonal moist evergreen forest, yet a small portion in the north contains secondary forest due to localized clearing for agriculture before the park was created in 1962 (WYB, pers. obs.). The secondary forest canopy is much lower and of a much more uniform height, and there are many fewer plant species in the understory (JFB, pers. obs.).

Sambar range from India to southern China, throughout most of mainland Southeast Asia, to some of the Sunda islands (Corbet and Hill 1992). They weigh roughly 109–260 kg (Lekagul and McNeely 1977), live in small groups, and are primarily browsers (Lekagul and McNeely 1977; Nowak 1999). Sambar are considered abundant in Khao Yai (Srikosamatara and Hansel 2000), though there are no quantitative density estimates there (Lynam et al. 2006). Red muntjac (also known as “common muntjac” or “barking deer”) are smaller animals (20–28 kg) (Lekagul and McNeely 1977) with a distribution similar to that of sambar (Corbet and Hill 1992). They are usually found in forests or dense vegetation, are usually solitary, and males establish scent-marked territories that overlap home ranges of females but not, generally, those of other males (Nowak 1999). They browse and graze (Nowak 1999), though fallen fruits can form an important part of their diet (Barrette 1977). Red muntjac are considered abundant in Khao Yai (Srikosamatara and Hansel 2000); camera-trapping studies suggest a population density in the Mo Singto area of 0.9–1.9 km<sup>-2</sup> (Lynam et al. 2006). Other ungulates recorded in the Mo Singto vicinity are the Asian elephant (*Elephas maximus*) and lesser mouse-deer (*Tragulus kanchil*) (Srikosamatara and Hansel 2000); gaur (*Bos gaurus*) are present in the park but neither the animals nor their sign have been observed within 1 km of the plot (WYB, pers. obs.). Little is known about the foraging behavior or dietary selection of ungulates in this system, but Smitinand (1977) provides a non-comprehensive list of plant species available for forage in Khao Yai.

Both sambar and muntjac consume large quantities of *Choerospondias axillaris* (Anacardiaceae) fruit during its fruiting season (June–October; JFB, WYB, pers. obs.). Aside from the two deer, *C. axillaris* fruits in Khao Yai are reported to be consumed only by gibbons (*Hylobates* spp.) and rodents (Kitamura et al. 2002). Sambar and muntjac regurgitate piles of clean, shiny *C. axillaris* pyrenes after rumination on their bed sites (JFB, WYB pers. obs.).

### Field methods and data analysis

We surveyed 15 belt transects on the forest biodynamics plot weekly for 10 weeks (mid-July through September) in 2003 and 2004. Each transect was 500 × 4 m, and together they covered 10% of the total surface area of

the biodynamics plot. On these weekly surveys we noted the location of deer bed sites using field sign (c.f. Teng et al. 2004); specifically, we located the presence of piles of regurgitated *C. axillaris* seeds and associated body imprints of the deer themselves. We identified the deer species that used the bed site by measuring the tracks and, if present, the scat associated with each site. We carefully removed the leaves surrounding the site and surveyed the ground beneath for hoof prints that had registered through the litter. Given the large size difference between muntjac and sambar, deer species identity could easily be ascertained by track or scat size (Srikosamatara and Hansel 2000; Kanjanavanit 2004). We did not use the sizes of the body imprints themselves to identify deer species because imprint size varies so much depending on the position in which the animal lay (JFB pers. obs.). At each bed site location we measured the canopy cover, slope, and aspect. Canopy cover proportion was ascertained by taking hemispherical canopy photographs at each bed site location using a digital Nikon D70 camera with a hemispherical fish-eye lens. These photographs were analyzed for canopy cover with HemiView 2.1 software (Delta-T Devices Ltd, Cambridge).

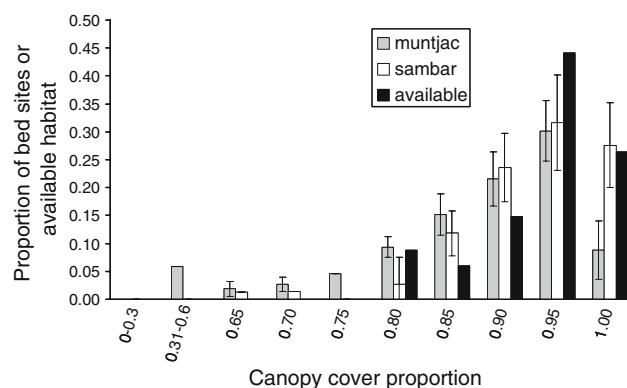
We compared deer bed sites in terms of canopy cover, slope, and aspect. There were several clusters in which 2–7 bed sites were found in close proximity (within 10 m). Since the bed sites in these clusters were almost certainly not independent, to reduce pseudoreplication we treated each cluster as a single site and measured habitat variables at the midpoint of the cluster. Canopy cover was treated as a continuous variable. Slope was treated as a categorical variable, broken into “low” (0–10% slope), “medium” (11–20%), and “high” (21–30%) groups. Aspect was also treated as categorical, broken into four groups: north (N), east (E), south (S), and west (W). For canopy cover proportion and slope, we tested for within-species differences across the 2 years, as well as differences between the two species, using two-tailed Student’s *t* tests with separate variance. For aspect, we assessed differences between years and between species using Chi-squared goodness-of-fit tests. We then assessed habitat use by comparing the distributions of bed site canopy cover, slope, and aspect with the distribution of “available” habitat using the Neu-Byers method (Neu et al. 1974; Byers et al. 1984). Specifically, we first compared the distributions of “used” versus “available” habitats using Chi-squared tests, then determined which (if any) specific habitat classes were used disproportionately to their abundance using Bonferroni confidence intervals (Neu et al. 1974; Byers et al. 1984). We measured “available” habitat by recording canopy cover at 375 systematically located photo points on the Biodynamics plot as well as slope and aspect at 762 points in a grid across the plot. We assessed the relationships among the habitat variables slope and canopy cover using Pearson’s correlations. Since aspect is a circular variable we could not test linear correlations of it versus the other variables, so we

assessed the relationships of aspect categories to slope and canopy cover using ANOVA. Results were considered significant at  $\alpha = 0.05$  and marginally significant at  $0.05 < \alpha < 0.10$ .

## Results

In 2003 we located 50 muntjac bed sites in 35 clusters and 21 sambar bed sites in 16 clusters. In 2004 we located 46 muntjac bed sites in 41 clusters and 20 sambar bed sites in 18 clusters. Canopy cover was not significantly correlated with slope (Pearson’s  $R = -0.088$ ,  $P = 0.363$ ). Aspect was not significantly related to canopy cover (ANOVA:  $F_{3,106} = 1.571$ ,  $P = 0.201$ ) and marginally significantly related to slope ( $F_{3,758} = 2.125$ ,  $P = 0.096$ ). The mean canopy cover proportion (i.e., ranging from 0 = completely open to 1 = completely closed) for muntjac bed sites in 2003 was 0.924 (SE = 0.008). Muntjac bed sites in 2004 were in significantly more open conditions ( $\bar{x} = 0.883 \pm 0.012$ ;  $t_{70.1} = 2.806$ ,  $P = 0.006$ ) than in 2003. The canopy cover of sambar bed sites did not differ between years ( $t_{30.4} = 0.845$ ,  $P = 0.405$ ), the mean for both years combined was 0.911 ( $\pm 0.010$ ). There were no detectable differences between the two species in the canopy cover of their bed sites (pooled across years:  $t_{75.2} = -0.730$ ,  $P = 0.467$ ). The distribution of bed site canopy cover was significantly different from the distribution of available habitat for muntjac ( $\chi^2_{14} = 43.601$ ,  $P < 0.001$ ) and marginally significantly different for sambar ( $\chi^2_{14} = 22.048$ ,  $P = 0.078$ ). Both species disproportionately avoided more open habitats for their bed sites (Fig. 1, Table 1).

There were no significant differences between years in the slope of bed sites for muntjac ( $t_{73.6} = 0.605$ ,  $P = 0.547$ ) or sambar ( $t_{25.9} = 0.343$ ,  $P = 0.735$ ). There were marginally significant differences in the slope of bed sites between the two species (pooled across years:  $t_{55.2} = 1.709$ ,  $P = 0.093$ ). The slope of muntjac bed



**Fig. 1** Distribution of muntjac and sambar bed sites in relation to available canopy cover proportion (ranging from 0 = completely open canopy to 1 = completely closed canopy). Error bars show standard deviation from 10,000 bootstrap iterations

**Table 1** Habitat use versus availability, with Bonferoni confidence intervals as per Neu et al. (1974) and Byers et al. (1984)

Category	Expected proportion of usage ( $p_E$ )	Muntjac		Sambar	
		Observed proportion of usage ( $p_O$ )	95% Bonferoni confidence interval for $p_O$	Observed proportion of usage ( $p_O$ )	95% Bonferoni confidence interval for $p_O$
Proportion canopy cover					
0.30	0.003	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.35	0.003	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.40	0.008	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.45	0.005	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.50	0.008	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.55	0.013	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.60	0.019	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.65	0.019	0.013	$0.000 \leq p_O \leq 0.052$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.70	0.027	0.013	$0.000 \leq p_O \leq 0.052$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.75	0.045	0.000	$0.000 \leq p_O \leq 0.000^*$	0.000	$0.000 \leq p_O \leq 0.000^*$
0.80	0.093	0.026	$0.000 \leq p_O \leq 0.080$	0.088	$0.000 \leq p_O \leq 0.231$
0.85	0.152	0.118	$0.010 \leq p_O \leq 0.227$	0.059	$0.000 \leq p_O \leq 0.177$
0.90	0.216	0.237	$0.094 \leq p_O \leq 0.380$	0.147	$0.000 \leq p_O \leq 0.325$
0.95	0.301	0.316	$0.159 \leq p_O \leq 0.472$	0.441	$0.191 \leq p_O \leq 0.691$
1.00	0.088	0.276	$0.126 \leq p_O \leq 0.427^*$	0.265	$0.043 \leq p_O \leq 0.487$
Percent slope					
0–10%	0.173	0.184	$0.078 \leq p_O \leq 0.291$	0.412	$0.210 \leq p_O \leq 0.614^*$
11–20%	0.475	0.539	$0.403 \leq p_O \leq 0.676$	0.353	$0.157 \leq p_O \leq 0.549$
21–30%	0.352	0.276	$0.154 \leq p_O \leq 0.399$	0.235	$0.061 \leq p_O \leq 0.409$
Aspect					
North	0.295	0.329	$0.194 \leq p_O \leq 0.464$	0.324	$0.123 \leq p_O \leq 0.524$
East	0.348	0.263	$0.137 \leq p_O \leq 0.389$	0.382	$0.174 \leq p_O \leq 0.591$
South	0.206	0.197	$0.083 \leq p_O \leq 0.311$	0.176	$0.013 \leq p_O \leq 0.340$
West	0.151	0.211	$0.094 \leq p_O \leq 0.327$	0.118	$0.000 \leq p_O \leq 0.256$

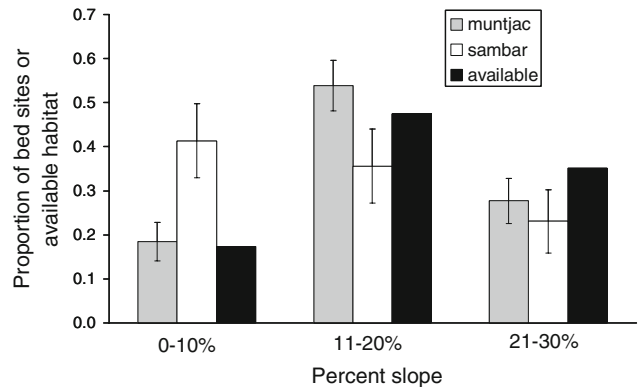
\*indicates a significant difference at  $\alpha = 0.05$ , where the available habitat proportion ( $p_E$ ) is not contained within the  $p_O$  confidence interval

sites was not significantly different from what was available ( $\chi^2_2 = 1.945, P = 0.378$ ). The slope of sambar bed sites was significantly different from what was available ( $\chi^2_2 = 13.545, P = 0.001$ ; Fig. 2); sambar disproportionately favored flatter areas for their bed sites (Table 1).

The aspect of bed sites did not differ between the 2 years for muntjac ( $\chi^2_3 = 5.645, P = 0.130$ ) or sambar ( $\chi^2_3 = 5.723, P = 0.126$ ). The aspect of the bed sites, for both years combined, differed between the two species ( $\chi^2_3 = 8.592, P = 0.035$ ; Fig. 3), with muntjac using a higher proportion of west-facing sites while sambar used east-facing sites. However, the aspect of bed site locations was not significantly different from the distribution of available aspects for either muntjac ( $\chi^2_3 = 3.673, P = 0.300$ ) or sambar ( $\chi^2_3 = 0.602, P = 0.896$ ).

**Discussion**

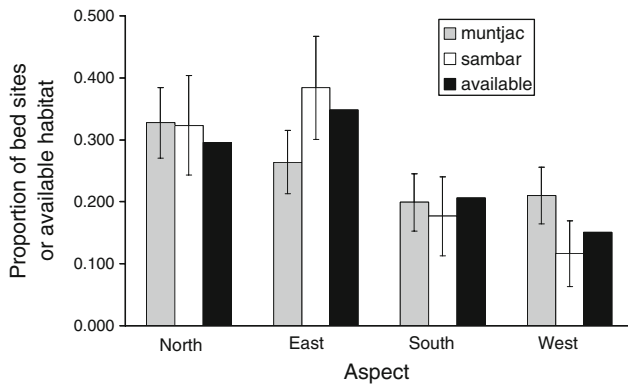
As with most deer, both muntjac and sambar appear to select bed site locations with high cover. Within the forest habitat surveyed here, bed site locations for both species were in areas of very high tree canopy cover; this may be either for concealment or to keep cool. Sambar also selected flatter areas for bed site locations, possibly



**Fig. 2** Distribution of muntjac and sambar bed sites in relation to available slope. Error bars show standard deviation from 10,000 bootstrap iterations

to reduce energy expenditures in travel to and from the sites or because flatter areas offer increased long-range visibility (Canon and Bryant 1997). We did not assess the bed site selection at the larger “between-habitat” scale, so we cannot determine whether muntjac in this system prefer grasslands over forests for bed sites as they do in Hainan Island (Teng et al. 2004). However, the grasslands in Khao Yai are artificially maintained by





**Fig. 3** Distribution of muntjac and sambar bed sites in relation to available aspect. Error bars show standard deviation from 10,000 bootstrap iterations

burning or mowing and generally lack shrubs for concealment.

Yet while the two deer species are similar in their choice of forest canopy cover, their bed site locations differ in aspect. Muntjac disproportionately select west-facing locations to bed, while sambar select east-facing sites. These differences could be due to the smaller, solitary muntjac avoiding the larger, social sambar. Alternatively, they could represent niche partitioning along an unknown resource axis.

Behavior and habitat selection by ungulates may also be importantly affected by human activities. Hunting is illegal in Khao Yai, and occurs only at low levels in the central portion of the park where this study took place (Lynam et al. 2006). Yet nearer the periphery of the park, hunting rates are much higher (Lynam et al. 2006) and in other parks they are so high as to have extirpated many large vertebrates (Round 1984; Maxwell and Elliott 2001). It is likely that muntjac and sambar bed site selection in those areas differs from that reported here, as the animals respond to this increased risk. Moreover, the assemblage of native predators may affect bed site selection. Tigers (*Panthera tigris*) are close to extirpation in Khao Yai (Lynam et al. 2006) and leopards (*P. pardus*) do not naturally occur there (Srikosamatara and Hansel 2000), though dhole (*Cuon alpinus*) remain relatively abundant (Srikosamatara and Hansel 2000; Lynam et al. 2006). Predator hunting mode (e.g., coursing versus ambush predation) has been shown to have very important effects on prey habitat selection (Schmitz 2008). Thus in parks where large cats (ambush hunters) are more abundant relative to dhole (coursing hunters), muntjac and sambar bed site selection may diverge from that reported here in response to different types of predation risk (c.f. Schmitz 2008).

**Acknowledgments** We thank the Royal Forest Department and the National Research Council of Thailand, and the chief and staff of Khao Yai National Park. Funding for this project came from a U.S. Environmental Protection Agency Science-to-Achieve-Results

fellowship, a U.S. National Science Foundation Doctoral Dissertation Improvement Grant, and Sigma Xi Grants-In-Aid-of-Research to JFB, by the Denver Zoological Foundation, the Universities of Montana and Washington, and by grants to WYB from the Biodiversity Research and Training Program, BIOTEC, Bangkok.

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