ECOLOGICAL OVERLAP OF
SYMPATRIC SUN BEARS AND ASIATIC BLACK BEARS
IN TROPICAL FOREST, THAILAND

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

Robert George Steinmetz

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

David L. Garshelis
Adviser

July 2009

ACKNOWLEDGEMENTS

DEDICATION

This dissertation is dedicated to my mother and father

—Donna and Robert Steinmetz—

and to the memory of my grandmother,

Betty Hubsch,

who loved wild animals

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Distinguishing Asiatic Black Bears and Sun Bears by Claw Marks on Climbed Trees

ABSTRACT Asiatic black bears (*Ursus thibetanus*) and sun bears (*Helarctos malayanus*) are sympatric in mainland Southeast Asia and face similar threats of habitat loss and commercial poaching. They are rarely seen but leave distinct signs, especially claw marks on climbed trees. These markings, which are potentially valuable indicators of presence, population status, and behavior of black bears and sun bears, have limited usefulness if the 2 species cannot be differentiated. I measured 121 claw mark imprints on climbed trees from 43 known (mainly captive) individual black bears and sun bears of both sexes in Thailand and Cambodia. The span across the markings made by 3, 4, or 5 claws from the hind foot was significantly greater for black bears than sun bears. I developed discriminant function models with these variables and arranged them in a 3-step process that distinguished claw marks as either sun bear, black bear, or indeterminate. This procedure correctly classified 95% of claw marks from the experimental animals. Tested on wild bears (at sites where only 1 species occurred), the procedure correctly classified 91% of claw marks of black bears in China ($n = 94$) and 100% of claw marks of sun bears in Indonesia ($n = 32$). The main limitation of the method was in distinguishing young, small black bears (cubs and yearlings) from sun bears. Nevertheless, application of these findings will be valuable in bear research and monitoring programs throughout Southeast Asia, where sign surveys have, until now, been hampered by the inability to differentiate these 2 ecologically and behaviorally similar species.

INTRODUCTION

Distribution and habitat use of Asiatic black bears (*Ursus thibetanus*; hereafter black bears) and sun bears (*Helarctos malayanus*) overlaps widely in mainland Southeast Asia. Both species occur in eastern India, southern China, Myanmar, Thailand, Laos,

Cambodia, and Vietnam, although they are not sympatric in all portions of this area (Servheen et al. 1999). Ecology of these tropical bears is little known, largely because their secretive, solitary nature and dense forest habitats make them difficult to study. Thus, even their presence in an area is often uncertain. Both bear species are threatened by commercial poaching (for their paws and medicinal gall bladders) and habitat loss that has reduced and fragmented populations (Servheen et al. 1999). Thus, it is a conservation priority to clarify the uncertain distribution and status of extant populations. Expense and complexity limit wide application, especially by local forest rangers, of technologically intensive methods such as radiotelemetry or genetic sampling, that are commonly used in studies of temperate bears. Sign-based methods have been applied extensively in Southeast Asia in status surveys and ecological studies of other large mammals but are not well developed for bears (Duckworth and Hedges 1998, Steinmetz 2004).

Sun bears and black bears leave signs, such as scats, tracks, holes dug into the ground, logs ripped apart, broken branches, and claw marks on trees, that reveal presence and activities. Most signs are uncommon or localized. For example, footprints are rarely found except in ideal substrates, and diggings are often spatially clumped. Black bears and sun bears are active tree climbers, and most signs typically found in the forest are claw marks on trees (Reid et al. 1991, Steinmetz et al. 1999, Hwang et al. 2002, Wong et al. 2002, Fredriksson et al. 2006). Relative ubiquity and long term persistence of claw marks makes them a potentially valuable tool for assessing status and ecology of bears. Presently, however, species-specific characteristics of these similar-looking signs are unknown, so the 2 species of bears cannot be differentiated. This limits investigations of even basic presence–absence information for these individual species in areas where they are sympatric, as well as areas where they were once sympatric but where one species has since been extirpated.

My objectives were 1) to determine whether Asiatic black bear and sun bear claw marks could be differentiated, and, if so, 2) to develop and test criteria for classifying claw marks encountered in the field as being from black bears or sun bears.

STUDY AREA

I obtained claw mark measurements of black bears and sun bears (mainly captive) of both sexes at several sites in Thailand and Cambodia, 2001–2005. Bears were kept in zoos (Lopburi Zoo, Phnom Tamao Zoo, Khao Khieow Open Zoo) or captive breeding centers (Banglamung Captive Breeding Center), which had outdoor enclosures with trees. Nearly all captive bears (31 of 33) had been taken from the wild and later confiscated by government authorities. I also obtained claw mark measurements from some wild adult sun bears ($n = 3$), adult black bears ($n = 3$), black bear cubs (10-12 months old, $n = 3$), and a sun bear cub ($n = 1$) in Thailand after observing these bears climb trees.

To test how well species differences discerned from claw marks of Thai and Cambodian bears could be applied to situations in the wild, I obtained claw mark measurements ($n = 126$) in other geographic areas inhabited by only 1 of the 2 species of bears. I obtained wild black bear claw marks in Tangjiahe Nature Reserve in the Min Mountains of northern Sichuan Province (32° N, 104° E), China. This area is north of the distribution of sun bears. I obtained claw marks mainly in mixed deciduous-coniferous broadleaf forest at 1,700–2,200 m. I obtained wild sun bear claw marks in tropical evergreen forest at 30–150 m in East Kalimantan (Indonesian Borneo, 1° S, 117° E) and at 800–1,100 m in Sumatra (1° N, 98° E), south of the range of black bears.

METHODS

Data Collection

To obtain samples of claw marks from captive bears, I fastened chicken meat, coconuts, or bananas to tree tops and released bears individually into the enclosure. After a bear climbed a tree I created a permanent template of its fresh claw marks by pressing a sheet of paper over individual sets of marks (i.e., marks from one foot) and punching holes with a pencil point over the center of each gouged mark in the trunk. If the mark was elongated from the claw slipping downward, I punched the hole at the point where the claw stopped slipping and gripped the bark, normally at the bottom of the mark. I obtained body masses and ages of the bears from captive records where available.

I created templates of only hind foot claw sets, which were recognized by their horizontal alignment (Fig. 1). The spread of each bear's hind foot marks was more

3

consistent than its front foot marks, which tended to be diagonally-oriented. I collected as many hind claw sets as possible from each bear. I then either painted or sanded tree trunks to cover that bear's marks and create a fresh surface for the next individual.

I obtained measurements from paper templates having at least 3 of the 5 hind foot claws on one foot. I measured straight-line distance (width) across sets of 3, 4, and 5 claw marks (Fig. 2), distances (and ratios of distances) between adjacent marks, and angles between lines connecting individual marks. Only the widths were useful in discriminating the 2 species. I measured 5-claw width (5cw) from toe 1 to 5. I measured 4-claw width (4cw) from toe 2 to 5 or 1 to 4, whichever was shorter. The imprint of toe 1 (innermost toe) generally registered lowest on the arc created by a claw set (Figs. 1, 2). I defined 3-claw width (3cw) as the measurement across the middle 3 marks (toes 2, 3, and 4) in a set showing all 5 marks; I did not use claw mark sets with only 3 marks unless their alignment (horizontal and tightly grouped; Figs. 1, 2) indicated that they were the middle 3 marks.

In China and Indonesia, where I obtained samples from wild bears, I created templates the same way, on claw-marked trees that I found opportunistically or during sign surveys. I used only marks that appeared fresh.

Data Analysis

I averaged measurements of all claw mark sets from individual captive bears to produce within-bear means for 5cw, 4cw, and 3cw, and then averaged within-bear means to derive species means. For templates from China and Indonesia, I considered each tree (from which I obtained ≥1 claw mark set) an independent sample unit, as I could not differentiate individual bears. Sun bears from the Asian mainland and Sumatra are similar in body size, whereas those in Borneo are smaller (Meijaard 2004). However, sun bear claw mark measurements from my samples in Sumatra and Borneo were not different ($P > 0.13$ for each variable) so I grouped data from these 2 areas.

I used boxplots to discern degree of species separation in claw mark widths from captive bears. I used 2-tailed t-tests to compare species-specific and sex-specific means. I used coefficients of variation to assess variability among individual bears. I assessed normality of data with box plots, equality of variances with Levene's test, and Box's M test to check homogeneity of variances for multivariate analysis.

4

I used discriminant function analysis on samples from the Thai and Cambodian bears to evaluate relative contribution of each variable (5cw, 4cw, 3cw) to species separation. I also used these functions to create a linear combination of variables that could be applied to identify species from claw marks in the wild. I compared 2 models. First, I conducted step-wise variable selection using Wilks's lambda to determine the order of entry of each variable and excluded variables that contributed least. In the second model, I entered variables together, without removal.

I evaluated the strength of my classification models in 2 ways. First, I determined the proportion of samples from captive bears that were correctly classified to species, using classification models developed from all samples and also using the more robust jackknife validation procedure, whereby I derived the discriminant function from $n-1$ sample cases and used it to classify the omitted observation (Landau and Everitt 2004). Second, I applied models derived from the mainly captive bear data in Thailand and Cambodia to templates obtained from wild bears of known species (in China and Indonesia).

RESULTS

I measured 59 claw sets from 20 black bears ($\bar{x}$ = 3 sets/bear) and 51 claw sets from 19 sun bears ($\bar{x}$ = 2.7 sets/bear) in Thailand and Cambodia, all ≥3 years old (hereafter adults). Additionally, I measured 8 claw sets from 3 black bear cubs and 3 claw sets from 1 sun bear cub. I obtained 94 claw sets, all on separate trees, from wild black bears in China and obtained 32 claw sets from 22 trees from wild sun bears in Indonesia.

Captive adult black bears had a mean mass of 120 kg for males (range 73–160 kg, n = 5) and 108 kg for females (63–150 kg, n = 5). Sun bears were smaller, averaging 61 kg for males (range 50–69 kg, n = 7) and 45 kg for females (range 21–58 kg, n = 12). I estimated mass of 2 black bear cubs whose claw marks I measured to be about 30 kg. I obtained no claw mark measurements from 1–2-year-old captive bears. However, the width across hind foot toes (not marks on trees) of some captive black bear yearlings (1-yr-olds) that I was able to measure ($\bar{x}$ =8.2 cm, SD = 0.84, n = 5) was equivalent to that of sun bear adults ($\bar{x}$ = 8.0 cm, SD = 0.91, n = 4).

Univariate Comparisons

Ranges in claw mark widths from adult Thai–Cambodian bears overlapped between the 2 species but interquartile ranges were well separated (Fig. 3). Claw marks of adult black bears were 29% to 33% wider than adult sun bears for 3cw, 4cw, and 5cw ($t_{37} > 4.7$ for each comparison, $P < 0.001$; Table 1). Claw mark variability was lowest (CV <13%) for 4cw in sun bears and 5cw in black bears (Table 1). In both species, 3-claw width had the highest variability. Within each species, claw width variables were highly correlated (pairwise combinations for black bears $r = 0.46$–0.75, $P < 0.007$; sun bears $r = 0.72$–0.83, $P < 0.001$).

Claw widths of Thai–Cambodian black bears (captive and wild) and wild Chinese black bears were similar (Table 1, $P = 0.19$–0.83). Sun bears from Thailand–Cambodia and wild bears from Indonesia had similar claw mark widths for 4cw and 5cw ($P = 0.81$–0.89), but 3cw of Thai-Cambodian bears was 13% larger than for Indonesian bears ($P = 0.04$). Mean claw mark widths for black bear cubs were close to those of sun bear adults for each variable (Table 1).

Claw marks of adult males of both species were 1% to 16% wider than females (Table 2), but differences were not significant for any measurement (3cw, 4cw, 5cw) for black bears ($t_{12} < 0.59$, $P > 0.56$) or sun bears ($t_{15} < 1.38$, $P > 0.19$).

Discriminant Function Analysis

Step-wise discriminant analysis differentiated the 2 bear species ($F_{1,37} = 49.2$, $P<0.001$). Wilks's lambda was lowest for 4cw (0.43), closely followed by 5cw (0.44), then 3cw (0.62). Four-claw width contributed most to group separation (canonical correlation coeff: 3cw, 0.69; 4cw, 1.0; 5cw, 0.77) and was the only variable selected to separate species.

The 4cw step-wise model correctly classified 87% of individual Thai-Cambodian bears to species (90% of black bears, 84% of sun bears): 2 black bears and 3 sun bears were misclassified. Classification accuracy was lower for individual claw sets (86% for black bears, $n = 3$ misclassified; 81% for sun bears, $n = 5$ misclassified) than when I averaged multiple sets from individuals. The jackknife validation procedure for the 4cw step-wise model produced the same classification accuracy as the original model for sun bears (individual bears and claw sets) and for black bear claw sets; however, the validation procedure produced poorer accuracy for black bear individuals

6

(85%). The step-wise model developed from Thai–Cambodian bears correctly classified 87% of wild Chinese black bears ($n = 12$ of 94 misclassified) and 100% of wild Indonesian sun bears.

Classification accuracy for the Thai–Cambodian sample was 5% lower for both species when I forced all 3 claw width variables into the model. Although 3cw and 5cw were not selected in the step-wise model, I evaluated their reliability in distinguishing species by creating models with each of these variables individually. Each variable differentiated the 2 bear species (3cw: $F_{1,37} = 22.4$, $P<0.001$; 5cw: $F_{1,37} = 46.8$, $P<0.001$). Three-claw width correctly classified 80% of black bears and 84% of sun bears; respective accuracy rates for 5cw were 80% and 74% for black bears and sun bears. Jackknife validation produced the same classification accuracy for each variable.

All Thai–Cambodian bears whose claw marks were correctly identified to species based on the 4cw model had high (absolute) discriminant scores (median: sun bears −1.15, black bears 1.21) and an associated high probability of membership in their respective groups (median: sun bears 0.97, black bears 0.96). In contrast, misclassified bears tended to have discriminant scores near zero and hence low probabilities of group membership assignment (median: 0.64). Scores for this low probability group were outside the 99% confidence intervals of discriminant scores for either species (Fig. 4).

I used the lower 99% confidence limit of black bear (0.382) and upper limit of sun bear (−0.583) discriminant scores for 4cw to distinguish samples with a low probability of correct classification into either bear group. With exclusion of this indeterminate group, overall accuracy of classification of Thai-Cambodian bears increased to 97% (95% for black bears, 100% for sun bears). However, some correctly identified samples ($n = 7$ of 34) fell into the indeterminate category and were thereby omitted by this process. Applying this procedure to 5cw and 3cw yielded a classification accuracy of 97% and 90%, respectively, for the Thai-Cambodia sample. With Chinese black bears, discriminant scores from 4cw measurements of 16 samples fell outside the 99% confidence interval and thus were considered indeterminate (5 of these would have been misclassified and 11 correctly classified). With these omitted, classification accuracy increased to 96%.

I combined the discriminant function equations for each claw mark measurement into the following 3-step process, whereby I compared each derived

discriminant score to its respective 99% confidence interval, thereby providing either a definitive or indeterminate classification. If either 4 or 5 claws in a set were available, I followed the process from step 1 (I measured 4cw from sets of either 4 or 5 marks; Fig. 2), progressing to steps 2 and 3 only if earlier steps resulted in an indeterminate classification. If the most complete claw mark set had only 3 marks, classification began at step 3.

1. Score1 = 1.257 (4cw) – 7.977
If score1 ≥ 0.382, classify as black bear;
if score1 ≤ –0.583, classify as sun bear;
otherwise, tentatively classify as indeterminate and check score2.
2. Score2 = 0.976 (5cw) – 8.344
If score2 ≥ 0.467, classify as black bear;
if score2 ≤ –0.423, classify as sun bear;
otherwise, tentatively classify as indeterminate and check score3.
3. Score3 = 1.552 (3cw) – 6.215
If score3 ≥ 0.148, classify as black bear;
if score3 ≤ –0.067, classify as sun bear;
otherwise, classify as indeterminate.

I simplified these equations through algebraic manipulation to produce a field-ready classification key (Table 3). Using this key, if widths of 4, 5, or 3 claw marks exceeded 6.6 cm, 9.0 cm, and 4.1 cm, respectively, the sign was classified as black bear; if less than 6.0 cm, 8.2 cm, and 4.0 cm, it was classified as sun bear. If widths did not fit any of these criteria, the mark was considered indeterminate.

Using this procedure, 95% of Thai–Cambodian bears were correctly classified to species. Applied to wild bears, the procedure correctly classified 100% of sun bear claw sets from Indonesia and 91% of black bear claw sets from China ($n = 8$ of 93 misclassified). Percent of bears correctly classified using this 3-step procedure was lower than that using just the first step because a few samples that were classified as indeterminate from the 4cw were classified to species, sometimes incorrectly, in steps 2 or 3. However, the 3-step process correctly classified a larger number of claw sets than did the 1-step process; the number left as indeterminate was reduced from 7 to 1 for

Thai-Cambodian bears and from 16 to 1 for Chinese bears (1/94 total samples = 1.1%) with the 3-step process.

DISCUSSION

Distinguishing Adult Black Bears and Sun Bears

Asiatic black bears tended to make larger claw mark sets on climbed trees than did sun bears, enabling most bears to be correctly classified to species. Four-claw width was the most important parameter for distinguishing species, due to its relatively low variability across individuals of each species (Table 1). Close correspondence between classification results of the step-wise discriminant model and its jackknife validation indicated that the classification function derived from the data set was reliable for prediction of unknown marks (McGarigal et al. 2000). Perfect accuracy could not be achieved, however, because ranges of claw mark measurements overlapped (Fig. 3). Variability in the data may have increased by my pooling of data from left and right claw mark sets.

Although a classification scheme based solely on measurement of 4cw was accurate in differentiating species, a non-trivial proportion of samples were categorized as indeterminate; additionally, all samples where only 3 claw marks were visible would be discounted, which could hinder studies where sample sizes are already small (low density bear populations or areas with few large trees). Instead, I recommend using a multi-variable procedure yielding fewer ambiguous cases. Multiple-variable models are, in general, expected to be less prone to misclassification, which in the case of bear claw marks might arise from variation in foot sizes, foot positioning on the tree, fissures in the bark, and measurement error. Accordingly, Zielinski and Truex (1995) recommended a more complex, 3-variable discriminant model to distinguish tracks of American martens (*Martes americana*) and fishers (*M. pennanti*), even though a single-variable model (with equivalent classification accuracy) would have sufficed. The correlated nature of bear claw mark variables, however, would be problematic for constructing one model that includes all measurements (Quinn and Keough 2002). Instead, my procedure used all 3 measurements (3cw, 4cw, 5cw) in separate, single-variable equations, which achieves a compromise between minimizing classification error and making use of all available information.

9

Sex and Age-related Considerations

Adult black bears are more than twice as massive as sun bears, but because sexual dimorphism is also quite pronounced in bears, large male sun bears and small female black bears could conceivably create claw marks similar to the other species (Lekagul and McNeely 1988, Stirling and Derocher 1990). In my captive sample, although male bears were larger and tended to create wider claw markings than females (Table 2), gender-related differences in claw marks were slight in comparison to species differences, possibly due to species-specific peculiarities in the structure of feet and claws and in climbing behavior. The misclassified bears in my Thai-Cambodian sample (using the 3-step procedure) included a female black bear and a large male sun bear (larger than would typically occur in the wild), and the one indeterminate animal was a male black bear.

Differentiating species may be more problematic for young bears. Black bear cubs at 10–12 months old had claw marks equivalent to those of adult sun bears (Table 1), even though the young black bears weighed less. My measurements of the feet of some live bears suggested that claw marks from black bears up to about 2 years of age could be similar to those of sun bears. Thus, the age structure of a wild bear population will introduce additional error, and classification accuracy of my method in field applications will likely be lower than the rates I observed with captive bears.

The China claw mark data provided an indication of potential error caused by young black bears misclassified as sun bears. Sun bear sized claw marks comprised 9% (binomial 95% CI 3–14%) of this sample (the misclassified portion of the data set). This suggests that in an area where the 2 species of bears are sympatric and roughly equal in abundance, given equal rates of tree climbing, the perceived number of sun bear marks could be inflated by about 8% (i.e., with 50% black bears, 9% of which are classified as sun bears, the perceived ratio would be 45.5:54.5 black bears:sun bears; thus 8% of the 54.5% perceived sun bear detections would be misclassifications). Error would be higher in places dominated by black bears and lower in areas more skewed toward sun bears (e.g., if the true ratio were 30:70 in favor of sun bears, the perceived ratio, with 9% misclassification of black bears, would be 27:73). Likewise, at montane sites in Thailand, which are inhabited mostly by black bears (Lekagul and McNeely 1988), 9% of claw mark samples that I collected in a companion study were sun bear

sized (*n* = 65, R. Steinmetz, Thung Yai Naresuan Wildlife Sanctuary, unpublished data); however, if some of these claw mark samples were truly from sun bears, the rate of misclassification would be somewhat less.

Incorporating error probabilities to define an indeterminate category (i.e., Table 3) should reduce misclassifications due to sex and age-related overlap between the species. In my sample of known black bear cubs, for example, one claw set fell into the indeterminate category, so it would not have been misclassified as a sun bear. Distinguishing claw marks of young black bears climbing a tree with their mother also would reduce their misclassification as sun bears.

Applications

Rigorous statistical analysis of track measurements has been used to distinguish the sex or individual identity of tigers (*Panthera tigris*; Sharma et al. 2003, Sharma et al. 2005), mountain lions (*Felis concolor*; Smallwood and Fitzhugh 1993, Lewison et al. 2001), pine martens (*Martes martes*; Zalewski 1999), and grizzly bears (*Ursus arctos*; Mattson 2003). Less commonly, such techniques have been used to distinguish different species, such as American martens from fishers (Zielinski & Truex 1995). My study, like these, offers a tool to facilitate indirect, sign-based investigations of endangered large carnivores.

In practice, distinguishing claw marks of these 2 species of bear depends not only on mathematical models, but also on the quality of sign encountered and treatment of that sign by the investigator. For example, sometimes multiple bears may have climbed the tree, creating different sized markings. Distinguishing separate climbing events, based on mark size, age, and ladder-like progression up the tree is necessary for accurate species identification.

If multiple claw mark sets are judged to be from the same bear, the investigator should record as many sets as possible and look for corroboration among the classification results. Occasionally, however, different claw sets from the same bear key to different species, due to variation among claw mark measurements; this occurred with 3 (7%) of my sample bears. Mis-matched claw sets could simply be regarded as indeterminate, unless a preponderance fit one species. Alternatively, because the variables in the 3-step classification process (4cw, 5cw, 3cw) are arranged in descending accuracy, a decision based on 4cw is more reliable than one based on 5cw,

11

and so on. Thus, for example, a case in which 4cw indicated black bear but 3cw indicated sun bear might be judged to be a black bear.

Investigators should be aware of 4 conditions of claw marks that reduce the probability of correct classification. First, old marks (> 1 yr) may be stretched by tree growth. Old marks can be easily distinguished by the widened gouges, and the presence of bark growth within or around the gouges. Second, deeply furrowed bark may shift the position of a bear's toes. Third, investigators may inadvertently measure front foot marks, whereas the criteria that I developed was based on hind foot marks. Bears stretch their front claws to grasp the sides of the tree trunk, creating variability in the spacing of the resulting marks, whereas they step straight up the tree (somewhat like ascending a ladder) with their hind feet (Fig. 5). Finally, marks created by a bear sliding down a tree may be spaced differently than for a bear climbing up or down. All of my experimental measurements were from climbing bears. Downward sliding marks are uncommon and readily distinguishable from the short marks (sometimes just holes) left by climbing bears (Fig. 1).

Compared to other potential survey techniques, bear claw mark surveys can be implemented without expensive equipment and with minimal training. I have found that those who regularly work in the forest can easily recognize bear sign, correctly create the paper template, measure claw widths, and use the 3-step reference table. Moreover, because a permanent record of the marks is created, the technique is less prone to measurement error than sign surveys that are reliant on field measurements (Mattson 2003). These virtues make this technique accessible, useful, and reliable for field personnel.

Remote cameras provide more accurate species identification than using claw marks. However, cameras require advance set-up and repeated checking, and may yield results that are biased by the specific sites chosen for the cameras. Moreover, the probability of detection is much higher for sign than with cameras: although I found plentiful bear claw marks at my study site in China, bears were not detected in an extensive camera-trapping effort there (Wang et al. 2006

MANAGEMENT IMPLICATIONS

My methods have at least 3 potential applications for research and conservation of bears. First, by distinguishing claw marks on climbed trees, investigators can determine distribution of sun bears and black bears in forested areas where the 2 species may be sympatric. As a corollary, in an area known to have bears, claw markings could help document absence or extirpation of one of the species. Second, claw mark surveys could be used to track changes in occupancy and relative abundance of each species within designated areas over time. Third, because tree climbing by bears is usually associated with foraging, claw mark data may yield insights into the feeding ecology of these species.

Table 1. Claw mark widths ($\bar{x}$ cm, SD) and corresponding coefficients of variation (%) from Asiatic black bears and sun bears measured in Thailand, Cambodia, Indonesia, and China, 2001–2005.

Area and species	No. of individuals[a]	No. of claw sets[b]	3-claw width			4-claw width			5-claw width		
			$\bar{x}$	SD	CV	$\bar{x}$	SD	CV	$\bar{x}$	SD	CV
Thailand and Cambodia											
Black bear adults	20	59	4.5	0.6	13.3	7.2	0.9	12.5	9.7	1.0	10.3
Sun bears adults	19	51	3.5	0.7	20.0	5.4	0.7	12.9	7.4	1.1	14.9
Black bear cubs	3	8	3.5	0.3	7.1	5.5	0.2	3.8	7.3	0.4	5.6
Sun bear cub	1	3	2.8			3.8			5.3		
Other areas											
Black bears (China)	94	94	4.7	0.8	17.0	7.3	0.9	12.3	9.6	1.1	11.4
Sun bears (Indonesia)	22	32	3.1	0.4	7.8	5.4	0.5	9.2	7.4	0.6	8.1

[a] For Thai-Cambodian bears, n = no. of individual bears; for other bears, n = no. of trees from which I took claw marks. I dwerectly observed bears making claw marks in Thailand and Cambodia (mainly in captivity). In China and Indonesia I only observed marks on trees, but in both these areas the species of bear was known because only one species occurred.

[b] Bears left multiple claw sets when they climbed a tree, only some of which were measurable. I averaged measurements for all sets for a given bear, or given tree, and then obtained means, SDs and CVs among these averaged measurements.

Table 2. Sex-specific claw mark measurements ($\bar{x}$ cm, SD) created by adult Asiatic black bears and sun bears that I observed climbing trees in Thailand and Cambodia, 2001–2005. Data are means of several claw mark sets per individual bear.

Species	Sex	n	3-claw width		4-claw width		5-claw width	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Sun bears	F	7	3.2	0.4	5.3	0.7	7.1	0.9
	M	10	3.7	0.9	5.4	0.8	7.4	1.3
Black bears	F	8	4.4	0.9	7.2	1.1	8.8	0.6
	M	6	4.6	0.4	7.3	0.7	9.8	1.3

Table 3. Field reference to classify Asiatic black bears and sun bears from measurements of hind foot claw marks on climbed trees. If either 4 or 5 claws in a set are detected, the reference is followed from step 1, progressing to steps 2 and 3 only if earlier steps result in an indeterminate classification. If the most complete claw mark set on a tree has only 3 marks, classification begins at step 3.

	Step 1	Step 2	Step 3
	4-claw width (cm)	5-claw width (cm)	3-claw width (cm)
Black bear	>6.6	>9.0	>4.1
Sun bear	<6.0	<8.2	<4.0
Indeterminate	6.0–6.6	8.2–9.0	4.0–4.1

Figure 1. Typical claw marks left by bears climbing trees in Southeast Asia. Both Asiatic black bears and sun bears are adept tree climbers and commonly make these signs.

Hind foot claw mark set

Front foot marks
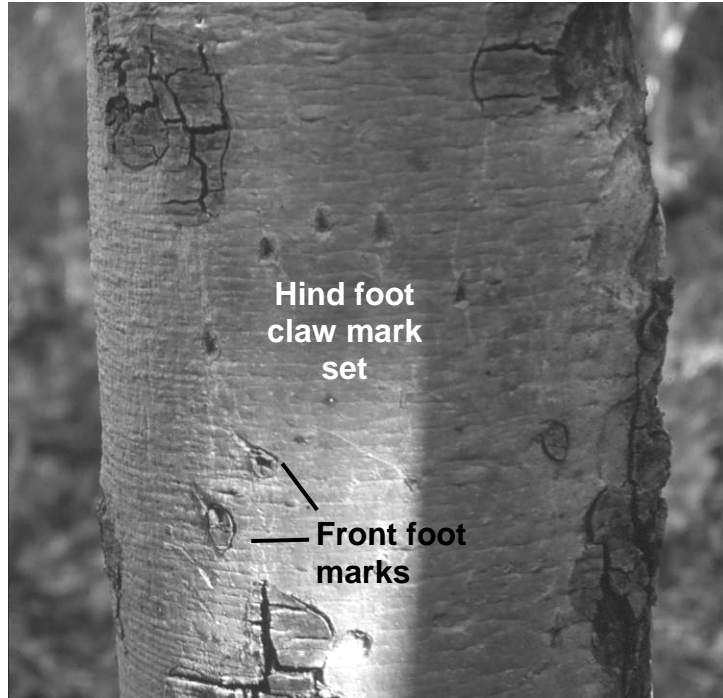
Figure 2. Representation of a bear claw mark set typically found on climbed trees, showing the arc of 5-claw imprints and measurements used to distinguish Asiatic black bears from sun bears. The claw set axis from hind foot marks is horizontal with respect to the tree trunk. The innermost toe (digit 1) is usually lowest, revealing which foot made the mark (right, in this case). I measured 3-claw, 4-claw, and 5-claw widths as the shortest straight-line distance between centers of gouged marks, as shown. Four-claw width could conceivably be measured from digit 1 or digit 5; I used whichever of these was shortest.
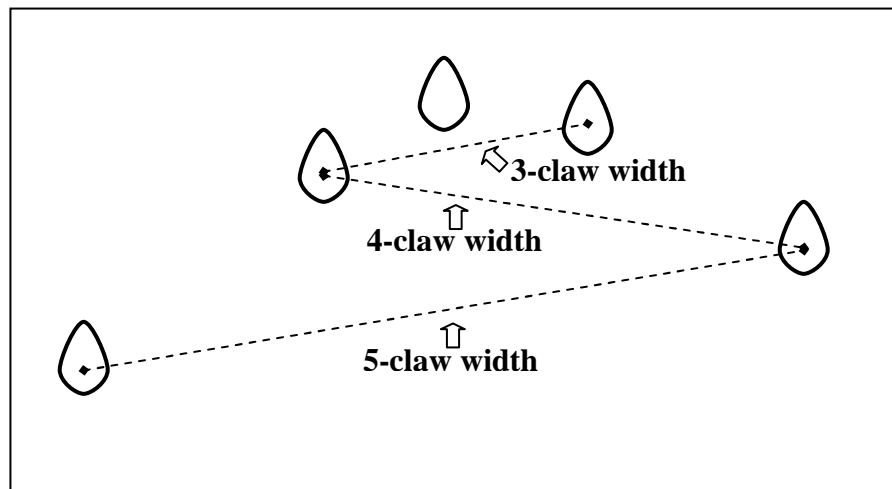
Figure 3. Widths of claw marks on trees created from 3, 4, or 5 claws of the hind feet of Asiatic black bears and sun bears in Thailand and Cambodia, 2001–2005, showing species and age class. range, interquartile range (box), median, and outliers (3-claw width only) for each

19
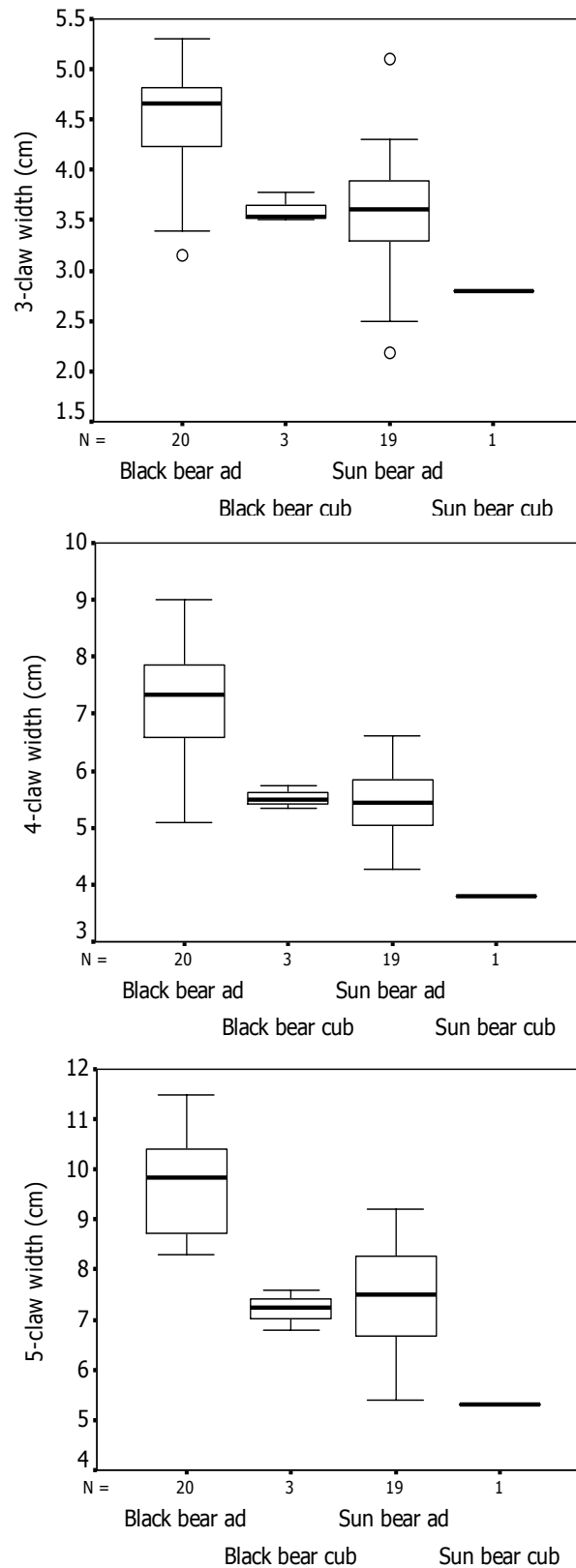
Figure 4. Mean scores (99% CI) from step-wise discriminant function analysis of claw mark measurements (4-claw width in this case) from adult Thai and Cambodian Asiatic black bears and sun bears (n = 39 individuals; both captive and observed in the wild, 2001–2005). Horizontal dashed lines delineate thresholds containing samples with a low probability of correct assignment to either species. Samples with scores in this region were defined as indeterminate.
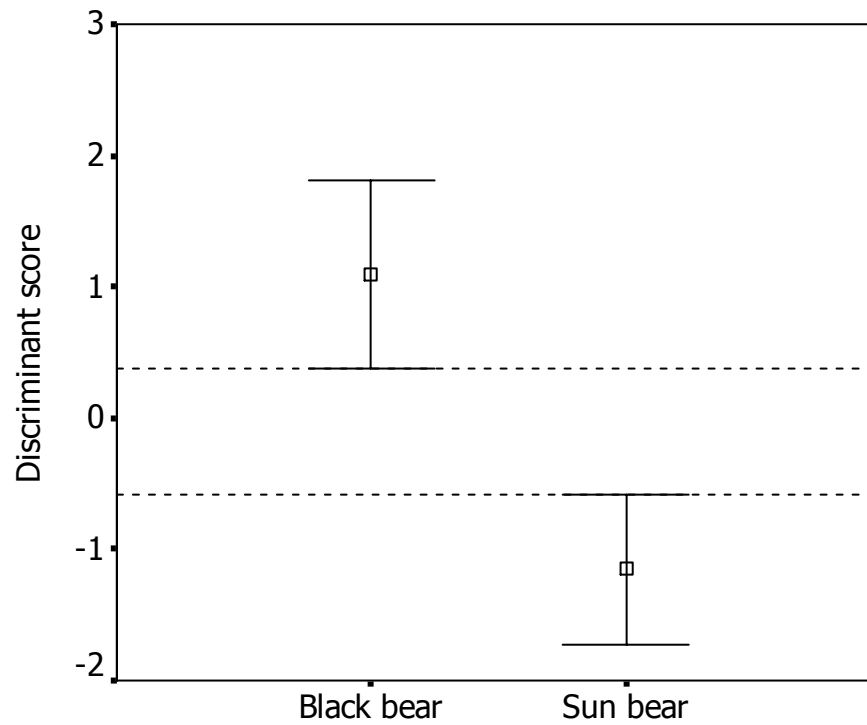
Figure 5. Bears climbing a tree, showing typical positioning of hind feet (stepping motion perpendicular to trunk) compared to front feet (diagonally grabbing the sides). Pictured are American black bears (*U. americanus*), but Asiatic black bears and sun bears use the same climbing technique. Because toes of the front feet spread apart when the bear is climbing, widths of hind foot claw sets are more consistent and more differentiable to species than front foot marks. (Photo: D. Garshelis)

Estimating ages of bear claw marks on climbed trees in Southeast Asian tropical forests

INTRODUCTION

Many large mammal species are difficult to observe directly so investigators often rely on animal sign as an indirect measure of distribution or abundance. Variation in sign decay rates among sites or over time is an important source of error in sign counts and can bias interpretations (Wemmer et al. 1996). Identifying the causes of heterogeneity in sign decay rates, and designing ways to account for this variation, can improve the accuracy of sign-based indices and strengthen inferences derived from them (Prugh & Krebs 2004, Sanchez et al. 2004, Brodie 2006).

Sign, especially claw marks on trees, is a useful tool for investigating presence, relative abundance, habitat use, and food habits of Asiatic black bears (*Ursus thibetanus*) and sun bears (*Helarctos malayanus*). These two species live sympatrically in forested habitats in Southeast Asia, where they are rarely observed. However, both species regularly climb trees to feed on fruits (Lekagul & McNeely 1977, Schaller 1969, Reid et al. 1991, Wong et al. 2002), leaving claw marks on the bark that are highly visible and, in some areas, prevalent (Duckworth et al. 1999, Steinmetz et al. 1999, Hwang et al. 2002). In a companion study I was able to differentiate which of the two species climbed a tree based on the width of the claw marks (spacing between toes; Steinmetz & Garshelis 2008).

Bear claw marks differ from most other animal signs (e.g., footprints, scats) in that they persist for a year or more, and their rate of degradation is mainly independent of environmental variables (e.g., rain, wind, insects). The long persistence of claw marks presents both opportunities and dilemmas for monitoring and researching bear populations. A benefit is that such sign provides a cumulative history of bear presence and activities. However, this cumulative record can be difficult to interpret, even deceiving, without knowing the age of the marks. For example, two areas with similar

densities of claw marks, one where they are mainly new and one where they are mainly old, suggest large differences in bear use. This paper presents the results of an experiment aimed to: (1) estimate ages of bear claw marks, (2) assess the effects of tree types and season on aging rates, and (3) develop guidelines that investigators can use to estimate age of bear claw marks in the wild and utilize this information for monitoring.

METHODS

Background and study site

This experiment emerged from opportunistic observations accumulated during sign-based surveys of large mammals over nine years (1994-2002) in protected areas in Thailand and Lao People's Democratic Republic. I commonly observed bear claw marks on trees during these surveys, and with time recognized 3 age categories, which I called fresh, recent, and old (Fig. 1). Fresh marks had sharply defined edges and loose (< 1 mm) woody grit inside the gouges. Recent marks had smoothed-over gouges, edges were no longer as distinct, and woody grit was absent. In old marks, bark had partly filled in the gouges, expanding up from the bottom of the mark and along its edges. The principle aim of this study was to match these physical differences with explicit time periods. To do this I monitored the aging process of actual and artificially-created claw marks.

The experiment was conducted in an 8-km^2 portion of western Thung Yai Naresuan Wildlife Sanctuary (3622 km^2), western Thailand (14°55'–15°45' N, 98°28'–99°05' E). Semi-evergreen and mixed deciduous forests occur in a patchwork across the area at elevations <1000m. I defined two seasons: dry (<100 mm rain per month; November to April), and wet (May to October). Mean annual rainfall (± SD) was 1592 ± 383 mm (Thai Department of Meteorology, 2005). Mean annual maximum and minimum temperatures were 33.7 ± 0.2°C, and 20.3 ± 0.7°C, respectively.

Experimental design

The experiment was conducted using 122 trees, from 17 families and 38 genera that bears were known to climb (R. Steinmetz, unpub. data). The tree families were: Anacardiaceae, Annonaceae, Dilleniaceae, Eleocarpaceae, Euphorbiaceae, Fagaceae,

Labiatae, Lauraceae, Leguminosae, Lythraceae, Magnoliaceae, Meliaceae, Moraceae, Myristicaceae, Myrtaceae, Sapindaceae, and Tiliaceae. Sample trees were in both evergreen and deciduous forest types, at elevations of 300-500 m. Large trees, 30-90 cm diameter at breast height (DBH), typical of those climbed by bears, were selected for study.

I created artificial bear claw marks on 85 trees by gouging the tree bark with a knife. Marks mimicked those of actual claw marks in thickness, depth, length, and spacing. Additionally, I monitored 14 trees that had actual marks from bears that I considered to be very fresh, and 23 trees with old marks from bears. Artificial and actual claw marks were monitored for 10-11 months, covering one rainy and one dry season. Most sample trees were monitored between July 2002 and July 2003, and additional samples were added and monitored between March 2004 and March 2005.

I returned to each tree approximately every two months (mean = 2.4 months, SD = 1.8) to classify marks as fresh, recent, or old (Fig. 1). If individual claw marks in a set of five matched different age categories, I assigned the set to whichever age category matched the majority of marks.

On most (65%) of the trees with artificial marks, I created a new set of marks at each recording event, resulting in a sequence of claw mark cohorts about two months apart. Side by side cohorts of varying ages served as a reference collection of mark conditions of known ages. A total of 212 fresh claw mark sets (real or artificial) in 9 cohorts were monitored during the experiment. For three cohorts the re-examination interval was 4–5 months, during which many marks had aged to the next stage and the exact month of age transition was therefore unknown. In such cases (42/212 = 21% of all claw sets), I treated the midpoint between revisits as the transition time (Martin and Geupel 1993).

I hypothesized that season, bark type, and wood hardness could affect the rate at which claw marks aged. Each claw mark set was categorized as to whether it was created in either the wet (n = 53 claw mark sets) or dry (n = 159 claw sets) season. Bark was categorized as thin (< 4 mm and generally smooth; n = 71 trees) or thick (> 4 mm, and generally furrowed, cracked, or flaky; n = 28). Wood was categorized as hard (n = 67) or soft (n = 32), according to species accounts in Chinh et al. (1996) and Gardner et al. (2000). If no published information was available, I used a machete to subjectively gauge hardness at a depth of ~1 cm. Wood density is sometimes

negatively correlated with a species' growth rate (Turner 2001), so I hypothesized that trees with softer wood would grow faster and cause more rapid aging (deterioration) of claw marks.

Data analysis

Two sets of analyses were conducted, one for the transition from fresh → recent, and another for the full age transition from fresh → recent → old. I estimated transition rates of claw marks using the Kaplan-Meier estimator with staggered entry (Pollock et al. 1989). Each claw mark set was treated like an individual animal in a survival analysis, and events (aging from fresh → recent, or fresh → old) were coded as 1 or 0. I plotted survival curves for graphical analysis and estimated median persistence times within age categories (i.e., number of months for 50% of samples to age to the next stage).

I tested whether survival curves differed according to season, bark type, and wood hardness, using log-rank tests (Krebs 1999). I also assessed the effect of each of these binary variables on the hazard rate (i.e., the rate at which marks changed to a different age category), by including them as covariates in a Cox proportional hazards regression. An important assumption of Cox regression is that hazard ratios of covariates are constant over time. I checked this assumption by testing the significance of interactions between a constructed time-dependent variable, and each of the three covariates (Ng'andu 1997). All covariates satisfied the proportional hazards assumption ($P > 0.11$ in all cases) except season in the full age transition ($P = 0.005$), so I stratified the Cox regression on season for analysis of fresh → old marks (Riggs & Pollock 1992). As a result, the effect of season in the full age transition could not be assessed directly by regression models, and I inferred the magnitude of its effect by comparing Kaplan-Meier seasonal survival curves. I examined four or five candidate models: a null model with no covariates, separate models with each covariate (except season in the full age transition), and a model with all covariates entered together. Log-rank tests and Cox regressions were conducted for each age transition, fresh → recent and fresh → old, separately. Many of my samples were not independent because they were repeat marks on the same tree.

Cox regression models were evaluated using Akaike's Information Criterion (AIC). For each model an AIC value was calculated, and models were ranked according to the difference from the lowest value (ΔAIC). For models with reasonable support

(∆AIC < 2.0), I calculated covariate risk ratios and their 95% CIs. Risk ratios measure the relative effect of a variable (e.g., soft or hard bark) on the transition to a different age category (Riggs and Pollock 1992).

RESULTS

Transition of marks from fresh to recent to old

All fresh claw marks progressed to the next age category (recent). Median time for this transition was 2.55 months. Most fresh marks (81%) had fine woody grit and sharp edges for at least 2 months, but after the third month 75% had aged into the recent category, and after 4 months only 6% still appeared fresh (Fig. 2a). Ninety-eight percent of fresh marks changed to recent within 5 months; only a single claw mark set still appeared fresh at the end of seven months.

Median time for transition of marks from fresh to old was 7.31 months. Most (78%) marks remained fresh or recent for at least 6 months, illustrated by the long plateau in the aging curve for that period (Fig. 2b). However, by 11 months, 90% of fresh marks had become old (Fig 2b).

Persistence of old marks

Most pre-existing old marks (69%) were still apparent after 11 months. Given that these marks were likely close to a year old when first observed, they were ≥2 years old by the end of the study. The other 31% of old marks had almost completely faded or were pushed out of the bark and would not have been detected without prior knowledge of their presence. There was no apparent relationship between disappearance of old marks and tree species (bark type, wood hardness).

Effects of season, bark type, and wood hardness

More marks (18%) created in the wet season appeared to transition to recent during the first 2 months than those created in the dry season (Fig. 2c), but by 3 months the aging curves for the two seasons matched, and overall the curves were not statistically distinguishable ($\chi^2 = 0.2$, $P = 0.65$, Table 1). Claw marks created in the wet season became old about 1 month earlier (median = 6.7 months) than marks created in the dry

season (median = 7.6 months, χ^2 = 9.38, P = 0.002, Table 1). Sixteen percent of marks created in the dry season were still considered to be recent after 11 months, whereas 100% of rainy season marks were old by that time (Fig. 2d).

Claw marks aged from fresh → recent slightly but significantly faster on trees with thin bark (median = 2.47 months) compared to thick bark (median = 2.70 months; log-rank test χ^2 = 5.0, P = 0.03; Fig. 2g, Table 1). Bark type did not affect transition time from fresh → old (Fig. 2h, Table 1). Wood hardness had no discernable effect on aging rates (χ^2 < 0.5, P > 0.5, Table 1; Figs. 2e,f).

For both age transitions, baseline (null) models that included no covariates fit the data well and received high support (low ΔAIC values) among candidate models (Table 2). Risk ratios were examined to further assess these covariates. Risk ratios for bark were < 1 (0.79 and 0.74 for age transitions to recent and old, respectively), implying a moderately decreased risk of aging for thick versus thin bark trees. However, confidence intervals encompassed 1.0 (Table 2), indicating that the difference was not statistically significant (Riggs & Pollock 1992). Risk ratios of ~1 indicated that wood hardness did not affect claw mark aging (Table 2).

DISCUSSION

This experiment demonstrated that ages of bear claw marks on climbed trees can be assessed by examining conditions of wound closure and bark growth in the marks (Fig. 1). Fresh marks have fine woody grit and distinct edges; these conditions last for about two months on most trees in western Thailand (Fig. 2a). By the third month, the fine grit disintegrates, marks become smooth, and the edges fade, marking the onset of the age category I referred to as recent. Sometimes recent marks have a threaded, striated appearance as new tissue spreads and hardens across the bottom. The recent stage is overtaken by bark or woody growth that fills in the mark and builds around the edges. These changes occurred predictably over a year across a wide range of tree species that encompassed divergent bark and wood characteristics.

Season and bark type affected aging rates of claw marks. Marks created in the rainy season aged slightly faster (Fig. 2d), probably due to greater soil moisture and hence tree growth and repair. Soil moisture is the major limiting factor for tree growth in tropical dry forest ecosystems such as Thung Yai (Turner 2001). Fresh marks on thin-

bark trees aged more rapidly than those on thick-bark trees in the transition from fresh → recent, but this effect dissipated over the longer transition to old. These effects of bark and season, although statistically significant, resulted in slight decay rate differences of less than one month and would not greatly affect mean estimates of claw mark age.

The similar decay rates of bear claw marks among different kinds of trees was probably attributable to the small size and depth of the marks, and fine scale features that I used to assess age categories, compared to the growth of the trees. Tropical forest tree species grow at rates of 0.5–6.0 mm in diameter annually (Turner 2001). Growth rates vary with moisture levels, but even in dry deciduous forests with <1000 mm of rain/year in Thailand, mean annual growth rates ranged from 0.8–2.4 mm (Sahunalu & Dhanmanonda 1993). Larger trees, such as the ones bears usually climb, tend to have higher growth rates: mean annual growth rate of 19 canopy species in semi-evergreen forest in Thailand was 0.5 mm for 30 cm DBH trees, 2.0 mm for 50 cm DBH trees, and about 4.0 mm for trees 80 cm in diameter (Kanzaki et al. 1995); thus claw marks are likely to age fastest on the largest trees. In this study, fresh claw marks on three very large (90 cm DBH) trees of the genera *Spondias* (Anacardiaceae), *Gmelina* (Labiatae), and *Lithocarpus* (Fagaceae), changed from fresh to old within just two months. These trees, however, were outliers: they were remnant, solitary individuals around one village and probably experienced exceptionally high growth rates due to the absence of competition for light and moisture. Nevertheless, this highlights the importance of microhabitat differences (e.g., proximity to clearings or waterways) that may affect growth rates and hence the mark aging processes on particular trees.

Claw marks persist longest in the old age class. Although I did not systematically monitor enough old marks long enough to estimate survival rates, my observations during study site revisits over several years indicated that old marks disappeared at variable rates, ranging from 2 to ≥5 years. Old marks in their second year and beyond often appear conspicuously puffy or stretched due to bark growth, and this feature becomes more pronounced with time. There are two main processes by which claw marks finally disappear: some are subsumed by growing bark and fade away, whereas others are physically extruded from the bark (Fig. 3).

Applications

This research creates opportunities for sign-based ecological research and population monitoring of bears. Bear claw marks are biologically meaningful because of their potential reflection of bear density and connection to feeding behavior and habitat use. Such data would be much better informed if the marks are categorized by age, and the age categories related to actual spans of time. Fresh sign is particularly relevant because it indicates that a bear visited the area and climbed the particular tree very recently, so one could link phenology to that specific feeding event (Wong et al. 2002, Fredriksson et al. 2006, Takahashi et al. 2008). In this study, >80% of sign still looked fresh after 2 months, but 75% did not look fresh after 3 months (Fig. 2a), indicating that fresh-looking sign on a tree encountered in the forest would likely be ≤2.5 months old. Recent sign tended to be 3–9 months and old sign ≥10 months to several years old. My finding that the mark aging process was minimally affected by season, bark type, and wood density indicate that these age guidelines are likely to hold for other similar forests in Southeast Asia; however, they would need to be recalibrated in other regions or other forest types.

An especially important use of sign age is in population monitoring (Karamanlidis et al. 2007). If estimates of the rate of tree climbing become available, they could be used in combination with sign decay rates to estimate actual bear density, as has been done with other species (Plumptree & Reynolds 1996). Sign production data could be obtained from human-habituated animals, although it is likely to be highly variable (dependent on fruit production), and thus imprecise. Instead, the ratio of fresh marks to older marks (recent + old) could be used as a metric by which to compare different populations or to track a population through time. For example, ratios increasingly dominated over time by older marks might indicate a declining population, whereas an area recovering from hunting should show increasing proportions of fresh sign. Sign density alone could be deceptive because old claw marks persist for such a long and variable time. A population index using sign density should be based on fresh and recent sign (omitting old sign), since these categories are little affected by variable survival.

The conspicuous bark growth of old marks makes them easy to identify, and easy to distinguish from fresh and recent marks (Fig. 1). Differences between fresh and recent claw marks are more subtle, and without experience and training an investigator

could confuse them. To avoid this problem, investigators could lump fresh and recent marks into a single category, compared against old marks. This would reduce error, and increase precision because more sign would be encountered (fresh sign typically accounts for a small portion of claw marks in the forest). The chief downside of lumping these two categories is the loss of ecological information (correspondence between climbing and phenology). Hence, I recommend attempting to distinguish all three categories for maximal utility, and lumping where appropriate for certain analyses.
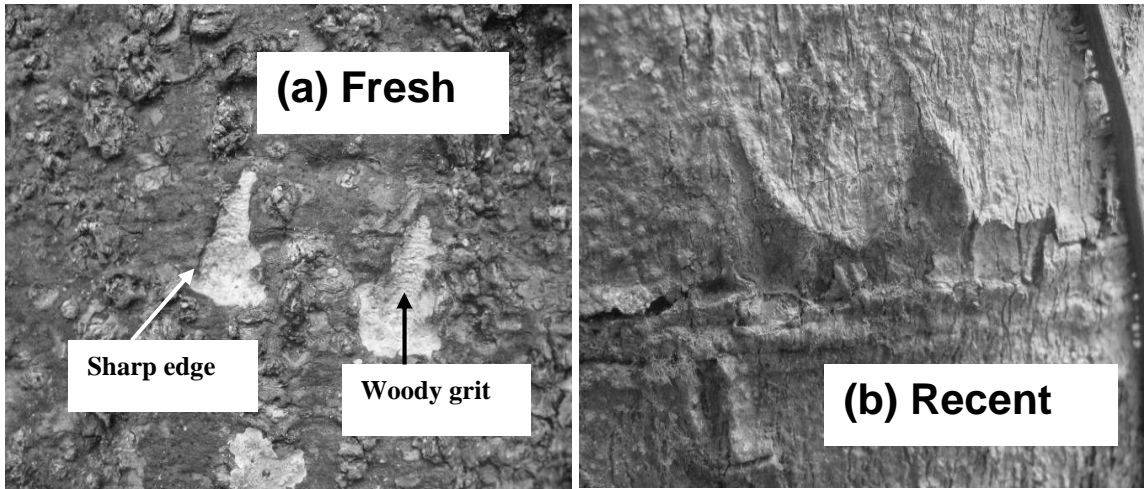
Figure 1. The aging process of bear claw marks on climbed trees, Thailand. Marks with fine woody grit and sharp edges are fresh, usually < 3 months old (a). Marks with smooth bottoms and rounded edges are recent, usually 3–9 months old (b). Marks with distinctive bark build-up inside and along the edges are old, usually ≥ 10 months old. Notice the fresh marks to the left of the old marks in (c); multiple ages of claw marks on the same tree suggest seasonal revisiting to feed on fruits in the canopy.
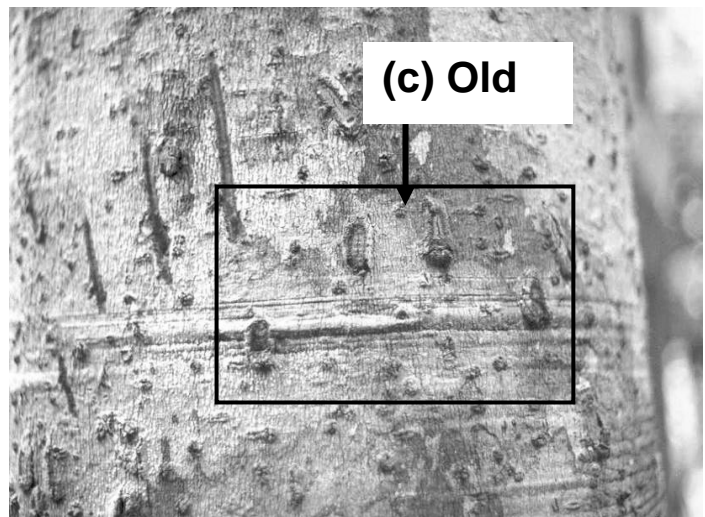
Figure 2. Estimated Kaplan-Meier survival functions of bear claw marks on trees in Thailand, 2002-2005. Survival curves estimate the proportion of claw marks persisting from one age category to another. Two age transitions are presented: fresh to recent (charts on the left), and fresh to old (charts on right). See text for definitions of age categories.

32
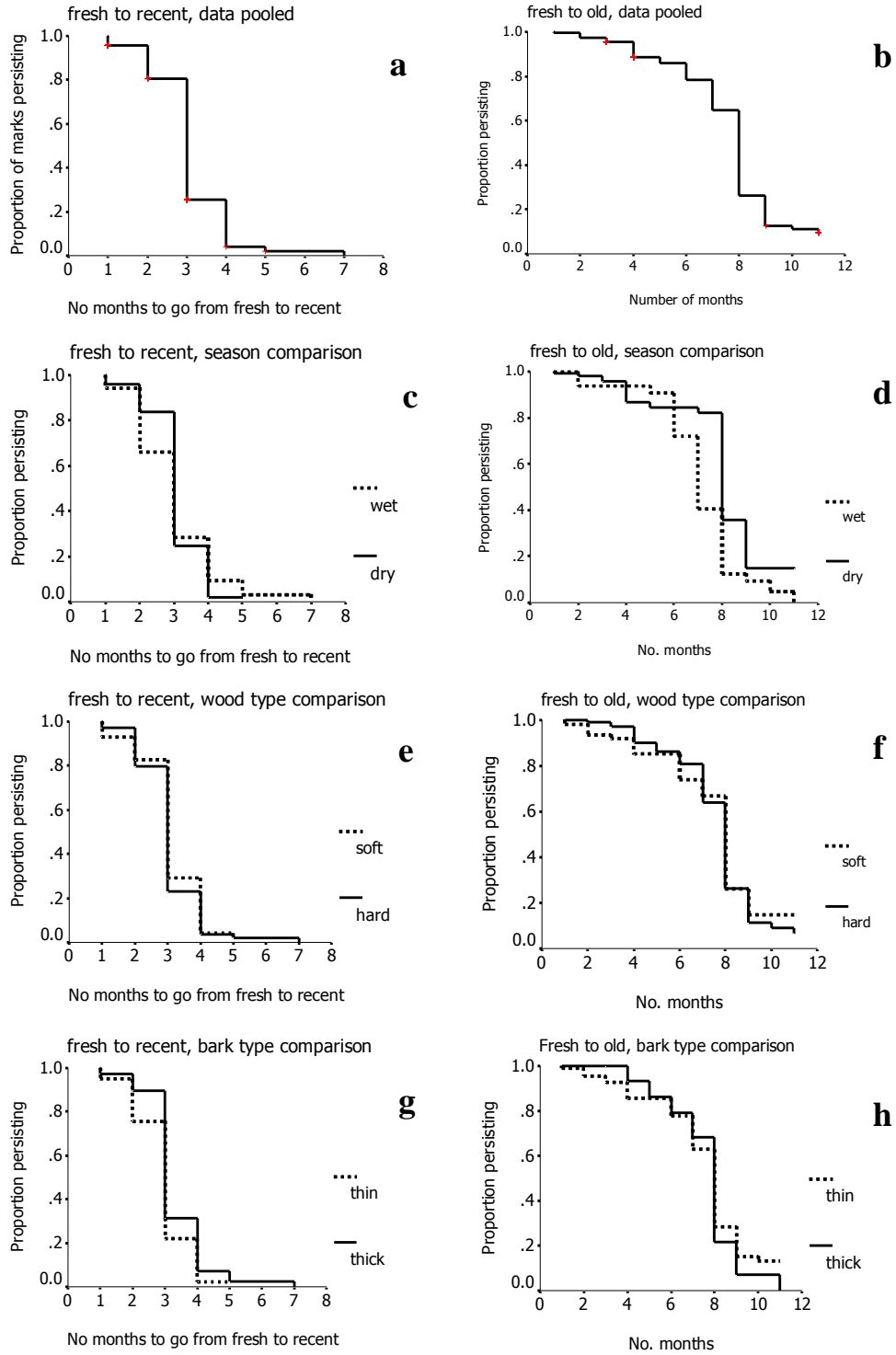
Table 1. Results of log-rank tests comparing Kaplan-Meier survival curves of bear claw marks on climbed trees in Thailand, 2002-2005. Curves were compared for season, wood hardness and bark type. Separate analyses were conducted for two claw mark aging transitions: fresh to

Age transition	Covariate	Condition	Median survival (months)	χ2	*P*
Fresh → recent	Season	Dry	2.53	0.2	0.65
		Rainy	2.33		
	Wood	Hard	2.51	0.46	0.49
		Soft	2.55		
	Bark	Thin	2.47	5.0	0.03
		Thick	2.70		
Fresh → old	Season	Dry	7.63	9.38	0.002
		Rainy	6.67		
	Wood	Hard	7.28	0.0	0.94
		Soft	7.32		
	Bark	Thin	7.30	0.01	0.94
		Thick	7.34		

recent, and fresh to old. df = 1 in all cases.

Table 2. Cox proportional hazards regression models describing the persistence of bear claw marks on climbed trees in relation to bark and wood type, and season (fresh to recent transition only), Thailand, 2002-2005. Abbreviations as follows: k, number of parameters; –2logL, –2 log-likelihood; AIC, Akaike's Information Criterion; ΔAIC, change in AIC. Models ordered from lowest to highest ΔAIC.

Age transition	Model	k	–2logL	AIC	ΔAIC	Risk ratio estimate	95% CIs
Fresh → Recent	Bark[a]	2	1605.88	1609.88	0.00	0.79	0.573–1.09
	Null	1	1607.99	1609.99	0.11	n/a	n/a
	Wood[b]	2	1607.79	1611.79	1.91	1.074	0.781–1.476
	Season[c]	2	1607.90	1611.90	2.02	0.943	0.636–1.398
	Wood + Bark + Season	4	1604.99	1612.99	3.11	*not considered*	*not considered*
Fresh → Old	Null	1	547.82	549.82	0.00	n/a	n/a
	Bark[a]	2	546.48	550.48	0.66	0.736	0.435–1.244
	Wood[b]	2	547.77	551.77	1.95	1.058	0.655–1.708
	Wood + Bark	3	546.44	552.44	2.62	*not considered*	*not considered*

a, Risk ratio estimate is for thick relative to thin bark.
b, Risk ratio estimate is for hard relative to soft wood.
c, Risk ratio estimate is for dry relative to rainy season.

Figure 3. Old bear claw marks in an advanced stage of deterioration (>1–2 years old). Individual gouges are eventually expelled from the surface of the bark. Photo by Gabriella Fredriksson.

Habitat use and interspecific relationship of sympatric Asiatic black bears and sun bears in a tropical forest mosaic

INTRODUCTION

Ecologically similar species are expected to compete, but can coexist by partitioning food, habitats, or times when they are active (Schoener 1986). Diverse habitat mosaics offer an axis of environmental heterogeneity along which species can partition themselves, and indeed selection of different habitats in a landscape appears to be a common mechanism of coexistence between similar species (Schoener 1974; Kotler & Brown 1988; Hanski 1995). Traditional ecological theory emphasizes that species separate through antagonistic interactions (Holt 2001), divergent niches (McGill et al. 2006), and distinct preferences (Rosenzweig 1991). However, patterns of habitat partitioning can also arise when species share preferences for a resource or habitat, but differ in their tolerances or competitive abilities, so become differentially distributed along an environmental gradient (Colwell & Fuentes 1975; Rosenzweig 1991; Wisheu 1998). Many communities appear to match this alternative model of organization (Wisheu 1998).

Asiatic black bears (*Ursus thibetanus*; hereafter, black bear) and sun bears (*Helarctos malayanus*) are sympatric across much of mainland Southeast Asia. Both species occur in northeast India, southern China, Myanmar, Thailand, Laos, Cambodia, Vietnam, and perhaps Bangladesh (Servheen et al. 1999). Within this region they co-occur ubiquitously at smaller spatial scales as well, such as in forest blocks and protected areas (Htun 2006; Vinitpornsawan et al. 2006). Sun bears, at 40–60 kg, are about half the size and mass of black bears (65–150 kg) (Lekagul & McNeely 1988), but are ecologically and behaviorally similar. Both species are opportunistic omnivores that share broadly similar diets of insects and fruit. They access fruit and insects by foraging

36

on the ground as well as climbing trees (Hwang et al. 2002; Wong et al. 2004; Fredriksson et al. 2006; Takahashi et al. 2007). Given their shared ranges and ecological similarities, how do these two species coexist?

Sympatric brown bears (*U. arctos*) and American black bears (*U. americanus*) may coexist principally through differences in habitat use: brown bears often use open habitats, whereas American black bears prefer forests (Aune 1994, Holm et al. 1999, Apps et al. 2006). These species exhibit morphological and behavioral differences related to these respective habitats (Herrero 1978, Mattson et al. 2005). In contrast, Asiatic black bears and sun bears seem much more similar in most traits: both have curved claws for climbing, neither seems markedly more aggressive than the other, and both are forest species. Asiatic black bears and sun bears have coexisted in Southeast Asia since the Middle Pleistocene (Erdbrink 1953, Tougard 2001), so mechanisms to reduce competition between them have had a long time to develop. For this reason, I expect any habitat partitioning between black bears and sun bears to occur subtly (Creel et al. 2001), perhaps involving body-size mediated tradeoffs among different forest types or along gradients of resource abundance across forest types. Forest cover in mainland Southeast Asia is comprised of a mosaic of evergreen and deciduous plant communities (Stibig & Beuchle 2003); this heterogeneity would appear to provide a natural basis for habitat partitioning to occur.

Using bear signs distinguished to species, I simultaneously sampled the occurrence of sympatric black and sun bears in a mosaic of deciduous and evergreen habitats in western Thailand. Most habitat use studies of large mammals rely on direct observation or radio-telemetry. Wild bears in Southeast Asia are rarely observed and difficult to capture, however, so I used incidence of bear sign to examine habitat use. Bear sign has been used to describe habitat use by brown bears (Clevenger et al. 1997; Poscillico et al. 2004), Asiatic black bears (Carr et al. 2002), and Andean bears (Cuesta et al. 2003; Rios-Uzeda et al. 2006).

Bears in Southeast Asia leave abundant sign in the forest which is conspicuous, long-lasting, and related mostly to feeding. Signs most commonly encountered are diggings and logs torn apart for invertebrates, and claw marks on trees climbed for fruit, rest, or refuge. Such signs result from behavioral decisions related to feeding or security, and thus are a good currency for quantifying habitat use and selection because they are linked directly to individual fitness. Bear signs are discrete 'event

sites'—places where animals have invested time and energy to accomplish important life functions (Buskirk & Millspaugh 2006). Sign data have been used to assess habitat use and co-occurrence for other sympatric carnivores (Wei et al. 2000, Alexander et al. 2006).

Animals respond to both local and landscape habitat features (Pedlar et al. 1997, Garshelis 2000, Bowyer & Kie 2006) so I analyzed habitat selection at two spatial scales. At a fine spatial scale, bears select feeding or resting sites within habitat patches. At a larger spatial scale, bears choose among patches across a landscape mosaic. I related occurrence of bears to habitat variables measured at these two scales: in proximity to event sites, and at a scale that corresponded to home range sizes of each species.

My first objective was to describe and compare habitat use by each species. Both species are threatened with extinction (Vulnerable; IUCN 2008), and this was the first ecological study of each in mainland Southeast Asia, so basic information on habitat use may inform conservation decisions. I also sought to determine specific habitat attributes selected by each species, and assess evidence for their interspecific competition. Measuring the effects of competition between species requires manipulative experiments (Schoener 1983) that are impossible for rare species such as Asiatic black bears and sun bears. As an alternative, I assessed competitive relationships by comparing their spatial distribution (e.g., Apps et al. 2006). If the two species of bears actively competed, I predicted they would (a) partition habitats, resulting in different patterns of sign abundance and distribution among different habitats, (b) select different habitat attributes, resulting in different models of habitat selection, or (c) avoid each other at small spatial scales, resulting in clustered incidences of sign for each species.

METHODS

Study site

The 3622 km^2 Thung Yai Naresuan Wildlife Sanctuary (15°00'–15°2 3' N, 98°30'–99° 05' E) is in western Thailand adjacent to Myanmar. The sanctuary is characterized by rugged mountainous terrain with elevations up to 1811m. Predominant forest types are mixed deciduous (45%), semi-evergreen (31%), and montane evergreen (15%)

(Nakhasathien & Stewart-Cox 1990). There are 3 seasons: cool and dry (November to February), hot and dry (March to May), and rainy (June to October). Mean annual rainfall (± SD) during the study was 1731 ± 217 mm (Thai Department of Meteorology, 2005), most falling between June and October. Mean annual maximum and minimum temperatures were 34°C and 21°C, respectively.

Semi-evergreen forest (SEF) and mixed deciduous forest (MDF) occur in a mosaic between 400 and 1000 m elevation. These habitats differ substantially in tree density, structure, and floristic composition (van de Bult 2003). Tree density (559 trees/ha), and basal area (43 m^2/ha) in SEF are almost twice that of MDF in Thung Yai (Webb 2007, R. Steinmetz, unpublished data). SEF is tall, with a closed canopy at 25-40 m formed predominantly by evergreen tree species (Maxwell 1995). Common families include Meliaceae, Dipterocarpaceae, and Annonaceae. MDF is dominated by deciduous tree species, including Leguminosae, Labiatae, and Bignoniaceae. Canopy height can reach 30 m, but tree density is lower and the mid-story more open than in semi-evergreen forest. Montane evergreen forest (MEF) occurs above 1000 m. It has high tree density like semi-evergreen forest but is floristically and structurally distinct. The families Fagaceae and Lauraceae are especially abundant, creating a closed, even canopy of lower stature than SEF. Density of termite mounds, a potential bear food source, is highest in MDF (5.3 ± 10.3/ha), lower in SEF (1.2 ± 1.7/ha), and near zero in MEF (R. Steinmetz, unpublished data).

Four study sites, 15–30 km apart, were sampled. Three were at 500–900 m elevation and contained mosaics of SEF and MDF; the fourth, at 1200–1800 m, contained MEF. Transects were distributed over an area of 30–100 km^2 at each site. The SEF and MDF sites were sampled 4 times between November 2001 and June 2003. The MEF site was sampled once, in March 2003. Sampling in SEF and MDF covered each of three seasons, and samples were pooled for analysis. MEF was sampled only in the hot dry season. I established multiple sites to maximize the number of individual bears that would be included in my population-level data. Annual home ranges of adult sun bears and black bears are 6–21 km^2 (Wong et al. 2004) and 30–150 km^2 (Reid et al. 1991; Hazumi & Koyama, in Garshelis 2004), respectively, and individual home ranges overlap widely. Thus, I expected the size and distribution of my study sites to reflect the activities of many individuals of each species.

39

Observations of bear sign

I searched for bear sign in straight, 300-m long strip transects within homogeneous patches of each forest type. To ensure good coverage of the forest mosaic at each site, I spaced transects at least 200 m apart. Transects covered the range of topographical variation within a study site (e.g., ridges, valleys). Transects were 10 m wide in SEF and MEF (0.3 ha) and 20 m wide in MDF (0.6 ha), commensurate with differing tree densities. In each strip, I closely examined the trunk of every tree (>10 cm DBH), looking for bear claw marks, and also searched the ground for holes or broken logs caused by bears foraging for insects. All ground signs of similar age in a transect segment (50 m) were grouped as one observation.

Distinguishing bear species and aging sign

When bears climb trees, they step up with their hind feet in ladder-like fashion, leaving distinct sets of marks corresponding to the five claws on each foot (meanwhile, the front claws generally clasp the side of the tree). When encountering claw marks, I pressed a piece of paper over a hind foot set and poked holes at each gouged mark. I measured the spacing of the claw marks (using only sets with at least three discernible marks) to classify whether the climbing event was by a black bear or sun bear. Previously, I conducted experiments in a captive situation to create a classification scheme, based on a discriminant function model, to distinguish the more widely-spread marks of black bears from sun bears. An overlap area (reflecting very small black bears or large sun bears) was categorized as indeterminant. This classification scheme was found to be 91–100% accurate when applied to bear-climbed trees in the wild (Steinmetz & Garshelis 2008). Bear marks that were old and stretched with tree growth, indistinct, or from front feet, were not identified to species. Bear footprints at insect-feeding sites were considered to be from black bears if hind pad width >10 cm and total length >17 cm, sun bears if measurements were below these thresholds, and indeterminate if length and width matched different species (R. Steinmetz, unpublished data from captive animals).

From previous experimental work (Steinmetz, Thesis chapter 2) I developed criteria to estimate age categories of claw marks: fresh (<3 months), recent (3–10 months), or old (>10 months). Bear diggings and opened logs that were accompanied by footprints were categorized as fresh (<1 month), because bear footprints do not

persist longer than 1 month (pers. obs.); all other insect-feeding signs were regarded as old (>1 month). Hence, I could separately analyze sign that was very fresh versus older.

Habitat variables

Local scale.—I measured six local scale variables: fruiting tree density, fruit abundance, canopy height, canopy cover, ground cover, and elevation. I counted the number of fruiting trees (trees bearing fruit during sampling) in each transect, and rated fruit abundance of each tree on a 1–4 scale (sparse to abundant). Canopy height, canopy cover, and ground cover were measured in two circular, 20-m diameter plots at 100 and 300 m along each strip transect ($n = 144$ plots total). I estimated canopy height to the nearest 5 m. Canopy cover, defined as percent of ground covered by the horizontal projection of tree crowns within the plot, was classified as <25%, 26-50%, 51-75%, or >75% (class midpoints were used for data analysis). I visually judged how well combined understory cover at 1 m height would hide a bear 10 m away, and assigned scores of 1 (very sparse) to 5 (very dense; i.e., a bear would be completely concealed) in four cardinal directions. Elevation was measured at transect centers.

Landscape scale.—Landscape scale variables represented the environmental conditions that surrounded transects. Using ARCMAP software and a GIS database for the wildlife sanctuary, I measured the distance from transect center to (1) streams, (2) habitat patch edge (an index of habitat heterogeneity), and (3) sources of potential human hunting pressure (villages, or seasonal roads, whichever was closer). I calculated habitat composition, defined as percent evergreen forest (SEF or MEF) relative to MDF, within circular areas corresponding to minimum and maximum home range estimates for each bear species: buffer radii, centered at transect mid-points, were 1.4, 2.6, 3.1, and 6.9 km.

Data analysis

Habitat use overview—Habitat use by bears was assessed as density of signs per hectare. Differences between bears within each habitat were tested with Mann-Whitney *U*-tests. I examined species-specific habitat patterns using fresh and recent signs. Within each bear species, differences in sign density among the three habitats were

evaluated using Kruskal-Wallis tests. SEF and MEF have higher tree density than MDF; since many signs were claw marks on trees, these habitats provided more opportunity for tree climbing and therefore higher sign density. Nonetheless, the data reflect differences in bear foraging behavior among habitats.

Next, I asked whether habitat attributes selected by each species differed. Habitat attribute means were calculated for transects with fresh signs of each species, and differences between bear species in each habitat tested with Mann-Whitney U-tests.

Habitat selection models.—I used logistic regression with forced entry to evaluate variables that distinguished used from unused transects for each species, and thus identify habitat components selected by each species. Habitat selection models were developed using only fresh signs.

To identify potentially important variables to include in regression models, I first used univariate Mann-Whitney tests to examine differences between mean values of each habitat attribute in transects with and without signs of each species. I selected variables with P-values <0.2 within each spatial scale (local and landscape). A high P-value was chosen because of the exploratory nature of the analysis.

A suite of 5-7 candidate logistic regression models, specific to each bear species, were ranked using Akaike's Information Criterion (AIC). The following models were considered: (1) all local and landscape variables, (2) landscape-level variables, (3) local-scale variables, (4) local-scale variables plus forest type as a categorical predictor, and (5) each variable selected by univariate tests. Additionally, for all local scale models I included fresh sign density of the other bear species as a surrogate for interspecific competition. If bears were competing, then one or both species might tend to occur where activity of the other species was lowest. Finally, I postulated that avoidance of black bears by smaller-bodied sun bears might depend on ground cover for concealment; therefore, for sun bears only, I included an interaction term between black bear activity (fresh signs/ha) and ground cover. Models were assessed based on lowest AIC scores and strength of evidence reflected in model weights, w_i (Johnson & Omland 2004).

I assessed fit of models to the data using Hosmer-Lemeshow Goodness-of-Fit tests and by examining standardized residuals. I used Cook's distance to isolate

individual cases that exerted undue influence on a model (Field 2005). Predictive power of models was assessed using classification success rates. I controlled for multicollinearity by checking tolerance scores of variables; where tolerance was < 0.2, I considered bivariate relationships with Spearman rank correlation and removed variables of lesser ecological relevance. I used regression slopes (*β*) and log-odds ratios to interpret the strength and direction of individual predictors in best-fit models.

Plot sizes were larger in MDF (0.6 ha) than in SEF and MEF (0.3 ha), possibly increasing the probability of detecting bear signs in MDF relative to other habitats. I examined the effect of plot size on regression results by entering plot size and the interaction between plot size and fruiting tree density. Resulting models showed no effect on probability of detecting bear signs for black bear ($\chi^2 = 3.09$, $P = 0.21$) or sun bear ($\chi^2 = 1.2$, $P = 0.55$).

Interspecific relationships.—I examined interspecific relationships in 3 ways. First, I tested whether occurence of each species was affected by foraging activity of the other species via logistic regression models. Second, I tested for nonrandom patterns of co-occurrence between bear species using *C*-scores calculated in EcoSim 7.0 (Gotelli & Entsminger 2001). The *C*-score index is $C_{ij} = (r_i - S)(r_j - S)$, where r_i and r_j are numbers of sites (transects) with species *i* and *j*, and *S* is the number of shared sites (Stone & Roberts 1990). This index measures the tendency for species to not occur together. In a community structured by competition observed *C*-scores should be larger than expected by chance (Gotelli & Entsminger 2001). Differences between *C*-scores observed and expected were assessed through Monte Carlo simulations that randomized the occurrence of each species among sites (5000 iterations), using EcoSim 7.0. I expected that if sun bears and black bears used sites (transects) independently of one another then *C*-scores should not differ significantly from random. I conducted separate tests for both fresh and within-year signs, to examine the short and long-term effects of potential competitors. Third, I used Spearman's rank correlation to test whether foraging activity by each bear species was inversely related to the other.

RESULTS

Habitat use overview

I conducted 38 transects in SEF, 27 in MDF, and 6 in MEF, covering 31.2 ha, and examined ~15,000 trees. I recorded 675 bear signs: 92.3% ($n = 623$) were climbed trees (not including trees climbed for bee nests) and 7.7% ($n = 52$) were insect feeding signs (including trees climbed for bee nests). Overall sign density from both species of bears was at least three times higher in evergreen forest types (SEF: $\bar{x}$ =33.8 ± 13.7 SD/ha; MEF: 37.8 ± 6.2) than in MDF (11.8 ± 6.0) (Table 1; Kruskal-Wallis χ^2 = 43.8, df = 2, P <0.0001).

Claw marks on climbed trees were the predominant signs in each habitat, comprising 84% (MDF) to 100% (MEF) of the samples (Table 1). Insect feeding signs comprised 16% of the sample in MDF, 6% in SEF, and 0% in MEF. Raided stingless-bee nests were 1.6 times denser in MDF than SEF (U= 416, P = 0.06), whereas terrestrial insect-feeding signs (dead wood opened, nests of ants and termites excavated) were almost three times denser in SEF (U = 503.5, P = 0.7; Table 1). I collected 33 bears scats opportunistically during the study (unidentifiable to species); 79% (n = 26) contained fruit; the remainder contained mostly insects (ants and beetles particularly).

Slightly less than half (44.7%) the claw marks on climbed trees were judged to have been created within the year (fresh + recent); 19% were fresh (created within 3 months). Thirteen of 27 (48%) terrestrial insect-eating signs and 4 of 25 (16%) stingless bee feedings were fresh. Of 648 climbed trees (including trees climbed for insects), 297 (45.8%) had claw marks that were sufficiently distinct and complete to measure for species classification: 160 were identified as sun bear, 129 as black bear, and 8 were indeterminant. Nineteen (37%) insect-feeding signs could be identified to bear species. This identified subsample was used to describe habitat use of each species.

Species-specific habitat use.— Fresh sun bear signs were over twice as abundant in SEF (2.7 ± 3.5/ha) compared to MDF (1.3 ± 1.4) or MEF (1.1 ± 1.7) (Fig. 1). Fresh black bear sign density, consisting solely of climbed trees, was over twice as high in SEF (1.9 ± 2.9/ha) and MEF (1.7 ± 1.8) as in MDF (0.8 ±1.1). These differences were not statistically significant for either sun bear (χ^2 = 1.98, df = 2, P = 0.37) or black bear (χ^2 = 1.81, df = 2, P = 0.41). However, considering sign up to a year old, foraging activity by black bears was significantly higher in MEF (13.9/ha) than SEF or MDF (χ^2 = 19.85, df =

2, P <0.0001), whereas sun bear activity was highest in SEF (9.2/ha; χ^2 = 27.23, df = 2, P <0.0001; Fig. 1).

Interspecific differences in habitat use.—Sun bears produced 19–37% more signs/ha than black bears in SEF and MDF (Fig. 1); differences were significant for within-year SEF signs (U = 480.5, P = 0.01), but not for other comparisons (P > 0.25). Conversely, black bears were predominant in MEF (Fig. 1): within-year black bear signs were five times more abundant than sun bears (U = 2.0, P = 0.009).

Most identifiable insect-feeding signs (16 of 19 = 84%), whether arboreal (stingless bees) or terrestrial (digging, log-opening), in both SEF and MDF, were from sun bears. Another 11 signs found off transects were from sun bears as well.

Univariate tests between mean habitat variables in transects with fresh signs of each species did not reveal any differences at either spatial scale ($P \geq 0.2$; Table 2). Thus, distributions of sun and black bears were not partitioned according to the habitat attributes I measured.

Habitat selection models

Univariate results.— Transects with black bear or sun bear climbing sign had more fruiting trees (7.8 ± 5.6 trees/ha; 7.4 ± 5.2 trees/ha for black and sun bears, respectively) than transects without climbing sign (5.7 ± 5.8; 5.9 ± 6.3) (U = 456.0, P = 0.06 for black bears; U = 499.5, P = 0.13 for sun bears). No other variables were identified as affecting use by either species (P > 0.2 in all cases).

Distance to edge of the habitat patch was especially variable among plots with and without fresh signs of each species (CVs: black bear, 106–112%; sun bear, 101–114%). This may have obscured the effect of this variable.

Logistic regression.—Elevation, percent evergreen forest, and fruit abundance index had tolerances <0.2 indicating problematic multicollinearity. I removed elevation, as it was correlated with canopy cover and fruit density, which are biologically more direct predictors of bear use. Fruit abundance index was correlated strongly with fruiting tree density; I retained the latter since it was less subjective and reflected similar information (food availability). Percent evergreen forest in small and large circular buffers were correlated for each bear species; I retained the larger buffer.

Standardized residuals of all models for each bear were between –1.6 and 1.3, indicating no points for which models fit poorly (Field 2005). No models deviated from a logistic fit (Hosmer-Lemeshow tests: $P > 0.12$). Cook's distance values were mostly very low (median 0.03–0.04), indicating few points with undue influence. However, in sun bear models Cook's distance was 3–6 times higher for MEF transects than all others, indicating undue influence on sun bear regression models (Field 2005). Therefore, I conducted regression for sun bear omitting MEF transects.

Fruiting tree density was the single best predictor of black bear and sun bear occurrence, and this attribute was included in the top three logistic regression models for each species, which accounted for 81% and 70% of model weights for black and sun bears, respectively (Table 3). For black bears, the best model (lowest AIC score) also included canopy height and distance to edge. Distance to edge was included with fruit in the second-best model for sun bears as well, but this had much less support (w_i = 26%) than the fruit-only model (w_i = 70%). For both bear species, there was little support for other local scale variables reflecting forest structure (canopy cover and height, ground cover), or for landscape-level variables related to disturbance, habitat composition, or water.

Both bear species tended to select transects with higher fruiting tree density. Slopes of best fit models (Table 4) suggested this effect was greater for black bears (β = 0.12, P = 0.03) than sun bears (β = 0.09, P = 0.09). Black bears also selected transects with lower canopy heights, though the effect of this variable was weaker than fruit (β = –0.1, P = 0.04). Distance to habitat patch edge had a negligible effect on black bear occurrence (β = –0.001; Table 4). The near-zero coefficient for distance to edge probably indicates no effect, despite appearing in the best model (Guthery & Bingham 2007). Classification success for top models was 62% for black bears and 65% for sun bears (Table 3). With no covariates, classification rates were 52% and 57%. Nagelkerke's r^2 values were 0.14 and 0.06 for black bear and sun bear top models, respectively.

Interspecific relationship

Within-year signs of black bears and sun bears were found in 50 (70%) and 57 (80%) transects, respectively; fresh sign of each of these species was found in 30 (42%) and 34 (48%) transects, respectively. Sixty-two percent of plots had within-year signs of

both species, and 21% had co-occurring fresh signs, similar to what would be expected by chance (product of the percent of transects with sign of each individual species: 70% x 80% = 56% for within-year sign; 42% x 48% = 20% for fresh sign). Accordingly, logistic regression models for each species that included fresh foraging activity of the other species received little support (Table 3). Likewise, co-occurrence of sun bear and black bear was not significantly different from random, for either fresh signs (C-scores: observed = 285, expected = 312.1; P = 0.46) or within-year signs (C-scores: observed = 126, expected = 144.3; P = 0.43). Though occurrence of each species was independent of the other, the extent of fresh foraging (signs/ha) by each species was negatively correlated (n = 49, r = –0.28, P = 0.05).

DISCUSSION

Habitat use

Despite substantial structural and floristic differences among the three forest types inhabited by bears in Thung Yai, in each of these habitat types, climbing of fruit trees was the main activity of both species that I could discern from their sign. Signs of insectivory in Thung Yai were rare, and insects appeared in a correspondingly low proportion of scats. In other parts of their range where sun bears feed mostly on insects, insect feeding sign is much more prevalent relative to climbed trees (Wong et al. 2002, Fredriksson et al. 2006); thus, this type of sign is visible where it does occur.

Insects were a relatively high proportion of the sign sample only in MDF (Table 1), perhaps compensating for lower fruiting tree density there (see Table 2), and correspondingly lower rate of tree climbing (Fig. 1). The higher density of opened logs in SEF may reflect higher tree density and thus more logs in SEF, plus periodic burning in MDF that reduces logs (pers. obs.).

Foraging activity of both species was concentrated in evergreen forest types, probably because evergreen forests have higher density and species richness of fruit-bearing trees than MDF (Bunyavejchewin et al. 2002, Webb 2007, R. Steinmetz *unpublished data*). Bears often concentrate their use of the landscape where food production is highest (Schoen 1990; Clark et al. 1994). Bear sign density should reflect animal use (time spent by individuals or number of individuals), so the significant

species-specific differences in habitat use (Fig. 1) suggest that, overall, black bears preferred MEF and sun bears preferred SEF.

However, within the shorter time frame reflected by fresh signs, differential habitat use was less pronounced, with each species creating about 1–3 signs/ha in SEF, MDF, or MEF (Fig. 1). This more equable short-term use among different habitats was reflected in regression results (which used only fresh signs): neither habitat composition nor forest type (as a categorical predictor) featured in habitat selection models for either bear species. This may indicate the importance of habitat heterogeneity for bears and the complementary nature of evergreen and deciduous forest types. Only 9% of fruit tree species used by bears were shared between MDF and SEF (R. Steinmetz, Chapter 4). Thus, each habitat provides a nearly unique assemblage of fruit, and in combination they offer a more diverse food supply than any one habitat. Habitat heterogeneity is important for frugivorous animals because it mitigates within- and between-year periods of fruit scarcity that typify tropical forests (Leighton & Leighton 1983, Whitmore 1998). Other studies have shown that American black bears benefit from having a mixture of habitat types within their home ranges (Costello & Sage 1994; Wooding & Hardisky 1994).

Of the 10 variables that I examined (including interspecific activity), only fruiting tree density was related to presence of feeding sign. Logistic regression might have failed to detect an effect (type II error) due to the general similarity between selected and available sites (James & McCulloch 1990; Garshelis 2000) (see Table 2). However, I believe the lack of effect of most variables indicates the general suitability of unused sites. For example, mean distance to water in SEF and MDF plots was only about 500 m (Table 2). This is probably an inconsequential distance for mobile bears; correspondingly, distance to water did not feature in logistic models. Similarly, potential hunting pressure (i.e., distance to roads, villages) was low in my study sites because of their remoteness and protection by rangers and village volunteers. Hence, cover was not as important a habitat component as where human activity is high (Landers et al. 1979). As with my study, other studies have also found that structural habitat variables had relatively little influence on bear habitat use, once food was accounted for (Davis et al. 2006; Rios-Uzeda et al. 2006). In North America, activity of American black bears was consistently concentrated in habitats with high fruit abundance (Costello & Sage

1994), and site selection by American black bears (Davis et al. 2006) and grizzly bears (McLoughlin et al. 2002) corresponded strongly to the availability of food.

The best models for each bear species explained low amounts of variation (low r^2), suggesting that bears selected attributes that I did not measure, or that my measurements were coarse. Another explanation is that bears ate fruits from the ground, resulting in instances of habitat use that went undetected. However, this would strengthen my main conclusion that fruit abundance was a strong predictor of bear occurrence.

Interspecific relationships

Signs of both species occurred in each forest type, so there was no evidence of strict habitat partitioning. However, signs of sun bears were more common than black bears in MDF and SEF, whereas the reverse held in MEF (Fig. 1). This pattern was consistent across temporal scales. Habitat use differences were most prominent in MEF, where black bear activity peaked at 14 signs/ha, and sun bears were rare despite abundant fruit (Table 2). These patterns may be indicative of some habitat partitioning, but the substantial overlap between species, especially in MDF and SEF, denotes a weak overall contribution from this potential mechanism of coexistence.

Sun bears and black bears shared a strong preference for fruit, and indeed the very same fruits (Steinmetz, chapter 4). These similarities resulted in extensive spatial overlap, whereby >60% of transects had signs of both species. Correspondingly, my models provided no evidence for strict avoidance. These results are supported by direct observations in Thung Yai. On three occasions both species were observed, directly or through camera-trapping, in the same vicinity just days, or, in 1 case, 2 months apart (W. Chutipong, *unpublished data*; Thung Yai rangers, pers. comm.). A similar pattern of spatial overlap prevails in Khao Yai National Park in Thailand (D. Ngoprasert, pers. comm.). Perhaps surprisingly, there is no evidence for direct conflict (fighting, chasing) or predation between the species. Clearly, at my study site and more widely in the region, sun bears and black bears regularly inhabit the same local areas within overlapping home ranges, yet avoid direct conflict. I believe bears accomplish this through active avoidance at fine spatial and temporal scales.

Although presence of each species was often independent of the other, fresh foraging activity (i.e. signs/ha) was inversely related. This result, while merely

correlative, suggests that within the shorter 3-month period represented by fresh signs, sun bears and black bears often avoided each other. Although not discernible from my data, I suspect that it is more likely that the smaller sun bears avoided black bears, than the reverse; smaller carnivore species typically avoid larger species (Creel et al. 2001). Since both bears selected high density fruit tree patches (Table 2), active avoidance suggests such patches were abundant in the forest, otherwise sun bears should be displaced to less productive patches with mean fruit densities lower than transects used by black bears.

Other studies that used more direct research methods have revealed similar instances of small-scale spatial avoidance by coexisting competitors that share similar diets. For example, radio-tracked spotted-tailed quolls (*Dasyurus maculatus*) and two other competing carnivore species regularly occupied small areas (about 1–2 km^2; inferred from map) simultaneously within overlapping home ranges without direct conflict (Glen & Dickman 2008), implying fine scale avoidance. Similarly, despite high densities and small, overlapping home ranges, bobcats coexisted with coyotes through spatial avoidance, probably using scent (Neale & Sacks 2001). Herbivores have similar relationships. Mule deer and elk strongly avoided each other over short time periods (6 hours), and this effect dissipated over a longer temporal window of 7 days (Stewart et al. 2002). This outcome closely matches my interpretation that bears avoided each other at short time scales but not over longer time periods.

Exclusive resource use—a mechanism of coexistence

One habitat (MEF) and one resource (insects) were used almost exclusively by each species (black bears and sun bears, respectively). Such exclusivity of use may enable each species to maintain sufficient densities, and hence co-existence, despite shared preferences for most of the other resources (Ritchie 2002). This idea stems from the concept of niche complementarity (Schoener 1974), whereby high overlap on one dimension is alleviated by low overlap on another. I propose that the one-sided use of insects and montane habitat promotes coexistence of these two species of bears, despite shared preferences for fruit and habitat overlap at lower elevations.

Though both bear species consume insects, accounts often describe sun bears as more insectivorous (Lekagul & McNeely 1988). Insects are the predominant food items for sun bears in Indonesia and Malaysia, except during mast fruiting events when

they are almost completely frugivorous (Wong et al. 2004; Fredriksson et al. 2006). Thus, although sun bears can subsist almost entirely on insects, they prefer fruit. Notably, when fruit is very scarce, even small sun bears may starve (Wong et al. 2005). In contrast, insects constitute a small proportion of diets of Asiatic black bears (0–4 % relative volume) throughout their range (Manjrekar 1989, Schaller et al. 1989, Reid et al. 1991, Hwang et al. 2002, Huygens et al. 2003). Sun bears, with their especially long claws, appear to be better adapted than black bears for digging insects; they also appear to be better adapted morphologically for obtaining the honey and larva of stingless bees (*Trigona* spp.). All predated nests of stingless bees that I observed were by sun bears. Accessing a nest requires many hours of strenuous effort, during which a bear bites and tears into a tree while clinging for long periods to the trunk. Sun bears have disproportionately large canines (Christiansen 2007) for chewing into trees, and a very long tongue for reaching the nest; moreover, their small body size enables them to more easily hang on the tree during the long period of excavation. The near absence of sun bears in higher-elevation forest in Thung Yai may be due, in part, to a paucity of insects there. Biomass and richness of ants and termites declines sharply with increasing elevation in the tropics, especially above 800 m (Collins 1989; Phoonjampa 2002), and reaches zero towards 1900 m (Collins 1980). I observed no termite mounds or bee nests in montane forest at my site.

Density of favored fruit trees is also exceptionally high in MEF, which may attract more black bears. Tree species richness, density, and basal area in Thai montane forests is dominated by Fagaceae (oaks) and Lauraceae (cinnamon), which are among the top three fruit tree families preferentially used by both sun and black bears in Thung Yai (R. Steinmetz, Chapter 4). Their combined density (> 10 cm DBH) reaches 138/ha in MEF, or 27% of stem density (Hara et al. 2002)—virtually every fourth tree in the forest is a potential food source. This is over twice the abundance of these families in SEF (61 trees/ha, 11% of stem density; Webb 2007). Interference competition would be intensified where preferred foods are concentrated in space. In North America, for example, larger brown bears exclude smaller American black bears from dense, defensible patches of food like salmon streams, berry patches, and cutworm moth (*Euxoa auxiliaris*) aggregation sites (Mattson et al. 1991; Aune 1994; Jacoby et al. 1999; Belant et al. 2006). In a similar sense, the high density of preferred fruit trees in montane forest in Thung Yai probably attracts relatively high densities of

black bears, making sun bears less able to use this habitat. Competitive coexistence is more likely when food density is low or intermediate (Holt & Polis 1997), which probably explains the greater overlap by sun and black bears in SEF and MDF compared to MEF. The MEF site also had sparser ground cover than SEF and MDF (Table 2), which could be another reason that sun bears rarely used it. Subordinate species often avoid open areas in favor of sites with denser cover that are safer (Creel et al. 2001), despite the denser sites being poorer in prey (Theberge & Wedells 1989).

In Sundaic Southeast Asia, where black bears are absent, sun bears occur up to at least 2000 m (Tumbelaka & Fredriksson 2006), and were frequently camera-trapped (100 photos in 4536 trap nights) between 700–1940 m in Sumatra (Linkie et al. 2007). Thus, the rarity of sun bears in montane forest in Thung Yai does not reflect any inherent constraint of the species. Rather, sun bears appear to be excluded due to a combination of habitat structure that creates defensible food patches, combined with the predominance of a larger competitor. This situation is perhaps intensified because insects, which are a supplementary food for sun bears, are largely unavailable, and ground cover is sparse. This interpretation should be regarded with caution, however, because my sample size in montane forest was small.

Limitations

My indirect sampling approach incurs three important limitations for the questions I addressed. First, both species of bears eat fallen fruit from the ground as well as by climbing trees (Hwang et al. 2002, Fredriksson et al. 2006). Because this behavior leaves little or no trace, a portion of feeding events were missed in my study transects. My interspecific comparisons implicitly assume that such terrestrial fruit feeding is similar for the two species. Second, the method that I used to distinguish black and sun bear claw marks, though accurate for adult animals (5% misclassification), often fails to distinguish between black bear cubs and sun bears (Steinmetz & Garshelis 2008). Thus, the sun bear portion of the sample is likely to be slightly inflated. Accounting for this possible inflation of sun bear sign would indicate that the use of SEF and MDF were even more equal for the two species, and use of MEF even more exclusive to black bears (see Fig. 1). My main conclusions—that habitat use by each species overlapped substantially in SEF and MDF but diverged strongly in MEF—are thus actually stronger than indicated by my data. Third, I could not assess whether temporal

partitioning contributed to the coexistence of bears. Diel partitioning of activity times can facilitate coexistence between competitors (Kronfeld-Schor & Dayan 2003). Bears in Thung Yai may alter their activity in response to the other species, as has been shown for other sympatric bears (Holm et al. 1999). I doubt, though, that temporal partitioning is fundamental to the coexistence of these two species, both of which have been observed or camera-trapped in Thung Yai diurnally and nocturnally, a pattern which appears to be widespread in Thailand (Grassman et al. 2006; Steinmetz et al. 2007).

Table 1. Signs of sun bears and black bears (species combined; all sign ages) recorded in sign transects ($n = 71$) in three forest types of Thung Yai Naresuan Wildlife Sanctuary, Thailand, 2001-2003. Insect feeding includes logs opened, and holes dug, for terrestrial insects. Stingless bees refers to excavated nests of *Trigona* sp. bees.

Sign type	Forest type								
	Semi-evergreen			Mixed deciduous			Montane evergreen		
	N (%)	Density	SD	N (%)	Density	SD	N (%)	Density	SD
Climbed trees	404 (94)	31.9	13.5	151 (84)	10.1	6.0	68 (100)	37.8	6.2
Insect feeding	17 (4)	1.6	3.4	10 (6)	0.6	1.2	0	0	0
Stingless bees	8 (2)	0.7	1.7	17 (10)	1.1	1.8	0	0	0
Signs combined	429 (100)	34.2	13.7	178 (100)	11.8	6.0	68 (100)	37.8	6.2

54

Table 2. Habitat attributes at sites where fresh signs (< 3 months) of sun bears and black bears were detected in Thung Yai Naresuan Wildlife Sanctuary, Thailand, 2001-2003. *P*-values are results of Mann-Whitney tests of differences between bear species. Overall habitat values are means across all samples. MDF: Mixed deciduous forest; SEF: Semi-evergreen forest; MEF: Montane evergreen forest.

Habitat	Spatial scale	Attribute	Sun bear		Black bear		*P*	Overall habitat	
			Mean	SD	Mean	SD		Mean	SD
MDF	Landscape	SEF in 6 km^2 buffer (%)	43.8	19.1	44.3	27.7	0.61	38.5	24.2
		SEF in 21 km^2 buffer (%)	55.3	11.2	51.4	21.6	0.78	49.4	21.0
		SEF in 30 km^2 buffer (%)	58.2	10.8	54.3	19.5	0.82	52.2	20.0
		SEF in 150 km^2 buffer (%)	59.7	8.5	56.6	10.3	0.36	55.8	11.2
		Distance to edge (m)	353	208	508	589	1.00	554	619
		Distance to water (m)	484	327	490	341	0.91	487	281
		Distance to disturbance (m)	3928	3829	2754	3513	0.82	3318	3551
	Local	Fruiting tree density (trees/ha)	5.6	3.9	5.8	3.6	0.96	4.6	3.8
		Fruit abundance index (0–4 per tree)	7.9	5.5	7.3	5.2	0.79	5.9	5.0
		Canopy height (m)	19.9	4.3	18.5	4.7	0.49	20.0	4.6
		Canopy cover (%)	36.5	10.8	34.1	14.9	0.87	34.0	12.5
		Ground cover (1 to 5)	3.6	1.4	3.5	1.5	0.95	3.6	1.4
		Elevation (m)	814	74	799	82	0.96	792	73.0
SEF	Landscape	SEF in 6 km^2 buffer (%)	79.8	19.7	76.4	20.5	0.61	76.4	21.1
		SEF in 21 km^2 buffer (%)	71.0	17.8	68.9	18.8	0.72	71.1	17.3
		SEF in 30 km^2 buffer (%)	68.9	16.9	67	17.9	0.66	69.4	16.8
		SEF in 150 km^2 buffer (%)	60.4	14.4	57.4	15.4	0.64	61.0	14.5
		Distance to edge (m)	783	755	724	699	1.00	765	717
		Distance to water (m)	512	391	579	321	0.66	518	371
		Distance to disturbance (m)	3885	3170	3470	2763	0.92	3788	3209
	Local	Fruiting tree density (trees/ha)	7.9	5.3	7.2	4.5	0.71	6.8	5.6
		Fruit abundance index (0–4 per tree)	4.5	3.1	4.3	2.8	0.88	3.9	3.4
		Canopy height (m)	27.7	5.2	26.7	5.0	0.53	27.5	4.4
		Canopy cover (%)	63.8	13.8	61.7	14	0.61	63.3	13.0
		Ground cover (1 to 5)	3.1	1.2	3.2	1.3	0.80	3.0	1.2
		Elevation (m)	822	72	819	79	0.45	817	69
MEF	Landscape	MEF/SEF in 6 km^2 buffer (%)	100	0.0	100	0.0	1.00	100.0	0.0
		MEF/SEF in 21 km^2 buffer (%)	100	0.0	100	0.0	1.00	100.0	0.0
		MEF/SEF in 30 km^2 buffer (%)	100	0.0	100	0.0	1.00	100.0	0.0
		MEF/SEF in 150 km^2 buffer (%)	98.9	0.14	98.9	0.12	0.74	98.9	0.1
		Distance to edge (m)	3193	161	3167	121	0.76	3191	184
		Distance to water (m)	891	270	826	222	0.36	842	207
		Distance to disturbance (m)	10611	865	10853	320	0.76	10453	489
	Local	Fruiting tree density (trees/ha)	13.3	9.4	18.9	5.1	0.37	13.9	9.0
		Fruit abundance index (0–4 per tree)	7.5	7.8	11.0	5.3	0.37	7.3	6.0
		Canopy height (m)	20.0	0.0	17.1	2.6	0.20	17.7	2.6
		Canopy cover (%)	68.8	8.8	66.7	7.2	0.74	64.6	16.6
		Ground cover (1 to 5)	1.5	0.0	1.5	0.5	1.00	1.3	0.4
		Elevation (m)	1560	28	1607	58	0.36	1593	41.3

Table 3. Comparison of logistic regression models of habitat attributes influencing occurrence of black bears and sun bears in Thung Yai Naresuan Wildlife Sanctuary, Thailand, 2001–2003. Fruit refers to density of fruiting trees. Local scale variables reflect conditions immediately around bear signs; landscape scale variables reflect surrounding environment in home-range sized circles around bear signs.

Bear species, Spatial scale	Model parameters	x^2	P	Classifi-cation rate (%)	AIC	ΔAIC	w_i
BLACK BEAR							
Combined	Fruit, Canopy ht., Dist. to edge	8.06	0.04	62	96.66	0.00	0.41
Local	Fruit, Canopy ht.	4.90	0.08	65	97.82	1.16	0.23
Local	Fruit	2.41	0.12	56	98.31	1.65	0.18
Local	Canopy ht.	1.81	0.17	59	98.83	2.17	0.14
Local	Fruit, Canopy ht., Canopy cover, Ground cover, Sun bear activity	5.60	0.35	66	101.11	4.45	0.04
Landscape	% SEF, Dist. to edge, Dist. to water, Dist. to disturbance	1.16	0.89	58	105.56	8.90	0.00
Local	Fruit, Canopy ht., Canopy cover, Ground cover, Sun bear activity, Forest type	7.56	0.37	68	107.16	10.50	0.00
Combined	All variables	9.32	0.41	61	107.40	10.74	0.00
SUN BEAR							
Local	Fruit	2.92	0.08	65	91.17	0.00	0.70
Combined	Fruit, Dist. to edge	2.97	0.23	62	93.12	1.95	0.26
Local	Fruit, Canopy ht., Canopy cover, Ground cover, Black bear activity, Black bear activity × Ground cover	3.87	0.69	66	98.22	7.05	0.02
Landscape	% SEF, Dist. to edge, Dist. to water, Dist. to disturb	1.59	0.81	55	98.50	7.33	0.02
Local	Fruit, Canopy ht., Canopy cover, Ground cover, Black bear activity × Ground cover, Forest type	3.88	0.79	66	102.21	11.04	0.00
Combined	All variables	3.23	0.98	58	117.07	25.90	0.00

Table 4. Parameter estimates of best-fit models describing habitat selection by sun and black bears in Thung Yai Naresuan Wildlife Sanctuary, Thailand, 2001–2003. Fruit refers to density of fruiting trees.

Bear species	Parameters	B	SE	P	Odds ratio	95 CIs
Black bear	Fruit	0.12	0.05	0.03	1.12	1.01–1.25
	Canopy height	–0.10	0.04	0.04	0.91	0.82–0.99
	Distance to edge	–0.001	<0.0001	0.09	0.99	0.99–1.00
	Constant	1.74	1.22	0.15	5.70	
Sun bear	Fruit	0.09	0.05	0.09	1.09	0.99–1.21
	Constant	–0.55	0.40	0.17	0.58	

Figure 1. Sign density of sun bears and black bears in three habitats of Thung Yai Naresuan Wildlife Sanctuary, Thailand, 2001–2003. Fresh signs (< 3 months) are a subset of within-year signs. Within year signs combine fresh and recent signs. Bars represent 90% confidence intervals.
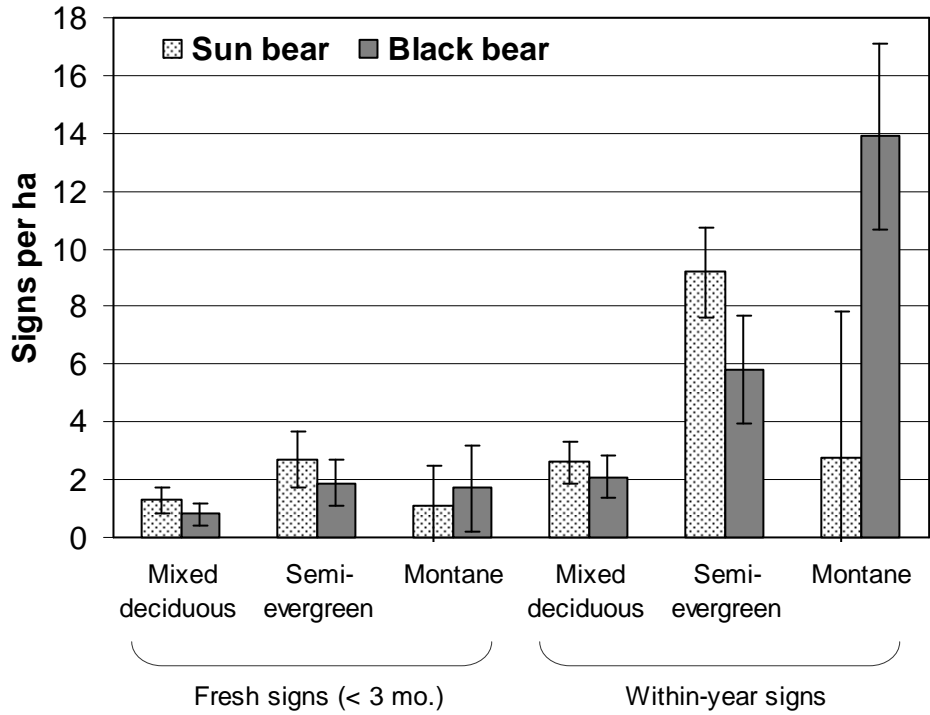
Feeding ecology and coexistence of sun bears and Asiatic black bears in a seasonal tropical forest, Thailand

INTRODUCTION

Coexistence of ecologically similar species is facilitated by niche partitioning, typically along the dimensions of food or habitat (Schoener 1974). Among sympatric carnivores, body size differences often relate to differential accessibility and use of different prey sizes, facilitating coexistence (Rosenzlig 1966, Gittleman 1985, Karanth & Sunquist 1995). At regional scales, carnivore species that differ more in size tend to overlap more in range, presumably because size differences diminish interspecific competition for food (Dayan & Simberloff 2005, Davies et al. 2007). Most large carnivores (i.e. > 20 kg) tend to take vertebrate prey greater than half their body mass (Carbone et al. 1999). The bear family, Ursidae, is a prominent exception to this pattern. Except for polar bears (*Ursus maritimus*), ursid species rely largely on non-vertebrate foods that are just a fraction of their mass.

Asiatic black bears (*U. thibetanus*) and sun bears (*Helarctos malayanus*) are closely related members of the bear family (Mazza & Rustioni 1994, Krause et al. 2008), and have co-occurred in Southeast Asia since the Middle Pleistocene (Erdbrink 1953, Tougard 2001). Presently, these species co-occur in Myanmar, Thailand, Cambodia, Vietnam, and portions of India and China (Servheen et al. 1999). Across this region they coexist ubiquitously at small spatial scales as well, such as in protected areas and forest blocks (Htun 2006, Vinitpornsawan et al. 2006). Sun bears (40–60 kg) are about half the size and mass of black bears (65–150 kg) (Lekagul & McNeely 1988), but despite this difference they are ecologically and behaviorally similar. Both species are opportunistic omnivores that share broadly similar diets of mainly insects and fruit. Additionally, they both access fruit and insects by foraging on the ground as

well as climbing trees (Wong et al. 2004, Fredriksson et al. 2006, Hwang 2002, Takahashi et al. 2008). Given these similarities, how do sun bears and black bears coexist so extensively in this region?

The aims of this study were to (1) provide the first description of the diets of sun bears and black bears in mainland Southeast Asia, (2) examine relationships between resource use by bears and resource abundance, and (3) assess evidence for resource partitioning that might explain species coexistence. To do this, I used sign transects to quantify the foraging behavior of bears in different habitats in western Thailand where these species are sympatric.

I examined three hypotheses regarding possible resource partitioning. First, bears might use different classes of resources. In allopatric portions of their ranges, black bears tend to eat mostly fruits and herbaceous vegetation (Hwang et al. 2002, Schaller et al. 1989), whereas sun bears, although also largely frugivorous, can subsist on insects when fruits are in short supply (Wong et al. 2002, Fredriksson et al. 2006). Thus, I posited that foraging signs of each species should be differentially associated with different food categories. Second, bears might partition resources through differential selection of the available fruit species. This hypothesis predicts that fruit selection patterns of each bear species should be distinct. I expected resource use overlap to be greatest when resources were least abundant, as bears would be forced to have similar diets (Wiens 1993). Third, bears might partition different fruit-crop sizes (analogous to prey size-class partitioning). Smaller-bodied competitors can coexist with larger species by foraging on smaller or less productive patches of food (Brown et al. 1994, Basset & Angelis 2007). Thus, this hypothesis predicts that larger-bodied black bears should select more abundant crops of fruit from larger trees, whereas smaller sun bears could exploit sparser crops in smaller trees.

METHODS

Study site

The 3622 km^2 Thung Yai Naresuan Wildlife Sanctuary (hereafter, Thung Yai) is in western Thailand adjacent to Myanmar. The sanctuary is mountainous, with elevations up to 1811 m. Two forest types, semi-evergreen and mixed deciduous, occur in a mosaic below 1000 m elevation and comprise 75% of Thung Yai's forest cover. Montane evergreen forest occurs between 1000–1800 m and is less extensive (15%).

Secondary forest, savanna, and dry dipterocarp forest comprise the remaining vegetation cover (Nakhasathien & Stewart-Cox 1990).

Semi-evergreen forest (SEF) is tall, with a closed canopy at 25-40 m formed predominantly by evergreen tree species (Maxwell 1995). Mixed deciduous forest (MDF), in contrast, is dominated by deciduous tree species, and tree density and plant species richness is lower than in SEF (Rundel & Boonpragob 1995, van de Bult 2003). Montane evergreen forest (MEF) has high tree density and richness like semi-evergreen forest but is floristically and structurally distinct, with the families Fagaceae, Lauraceae, and Theaceae especially abundant.

I defined two seasons, dry (November to April) and rainy (May to October). Rainfall is typically <100 mm/month in the dry season. Mean annual rainfall (± SD) in western Thung Yai during my study was 1731 ± 217 mm (Thai Department of Meteorology, 2005). Mean annual maximum and minimum temperatures were 33.6 ± 0.2°C and 20.5 ± 0.7°C, respectively. The pattern of seasonality during my study was almost identical to that exhibited on a longer, 9-year time scale (1997–2005), indicating that it was typical for the area.

I established four study sites; three contained mosaics of SEF and MDF, and the fourth was MEF. Sites were 15 to 30 km apart. Sign transects and vegetation plots were distributed over an area of 30–100 km^2 at each site. I established multiple sites to maximize the number of individual bears that would be sampled. Annual home ranges of adult sun bears and black bears are 6–21 km^2 (Wong et al. 2004) and 30–150 km^2 (Reid et al. 1991; Hazumi & Koyama, in Garshelis 2004), respectively, and individual home ranges overlap widely.

Most fieldwork was conducted during 12 expeditions from November 2001 to June 2003, covering each season at least once (except the MEF site, sampled once in March 2003). My data reflect bear activity and resource use over this 20-month period. Additional vegetation sampling continued until July 2005.

Determining bear diets

Observations of feeding sign.—Diets of bears were determined from observations of feeding sign and scat analysis. I searched for bear signs in 71 straight, 300-meter long, strip transects (n = 38 in SEF, 27 in MDF, 6 in MEF; total 31.2 ha). Transects were 10 m wide in SEF and MEF (0.3 ha) and 20 m wide in MDF (0.6 ha). Wider transects were

used in MDF because tree density was lower in that habitat. To ensure good coverage of the forest mosaic at each site, I spaced them systematically at ≥200 m apart. Transects covered the range of topographical variation within a study site.

I observed two main categories of bear sign: claw marks on climbed trees, and terrestrial insect-feeding signs (holes dug for nests of wasps, ants, and termites; raided termite mounds; broken-apart rotten logs). These signs have similarly long (many months) persistence times (G. Fredriksson, unpub. data; R. Steinmetz, Chapter 2); thus, differences in their relative abundance should reflect bear foraging behavior and not differences in decay rates between types of sign. Transect were divided into six 50-m segments, and insect signs of similar age in a segment were grouped as a single observation. I considered holes to be dug by bears if accompanied by footprints, or if deeper than 30 cm; other mammals make shallower digging signs (pers. obs.). I closely examined every tree (>10 cm DBH) within transects for signs of climbing, and measured DBH of climbed trees. Trees were identified in the field if possible based on Gardner et al. (2000). Leaf samples, and fruit or flowers if available, were collected for identification at herbaria in Thailand. Resource use by bears was expressed in terms of density of feeding signs (climbed trees/ha, insect-feeding events/ha).

I collected scats in the course of sign surveys and hiking in the sanctuary. I recorded frequency of occurrence of different food items, FO_i (%) = $(n_i/N) \times 100$, where N was the total number of scats and n_i the number of samples containing food item i. I did not attempt to differentiate scats to bear species.

Claw mark ages and species identification.— I categorized claw mark ages as fresh (<3 months), recent (3–10 months), or old (>10 months), based on an experiment (2001–2002) where I identified physical changes in claw marks over time (R. Steinmetz, Chapter 2). Claw mark ages were used to match fresh climbing with current fruiting in a tree, and identify whether multiple claw mark ages occurred on a tree.

Claw marks from Asiatic black bears tend to be larger than sun bears. The widths of sets of hind-foot claw marks (a group of 3–5 claw marks from the foot of a bear) were measured and classified as either black bear, sun bear, or indeterminate, based on a discriminant function model developed from captive bears (Steinmetz & Garshelis 2008). Bear marks that were old and stretched with tree growth, incomplete (<3 claws imprinted on the bark), or from front feet, were not identified to species. Thus,

I had two samples, one of all climbed trees irrespective of bear species, and a subset of that in which the bear species was identified and the marks were created mostly within the year (fresh and recent). The species-specific dataset was used to assess fruit-tree selection by each bear species, and hence niche overlap. The larger, species-combined dataset, which included many trees marked at least one year in the past, was used to examine general relationships between tree abundance and use by bears. Bear footprints at insect- or vegetation-feeding sites, where present, were classified as black bear if hind pad width was >10 cm and total length >17 cm, sun bear if measurements were below these thresholds, and indeterminate if length and width matched different species (R. Steinmetz, unpublished data from captive animals).

Assessing bear frugivory.—Claw marks on climbed trees were the predominant sign type. Sun bears and black bears may climb trees to feed, rest, and escape danger. I considered climbing to be associated with feeding if (1) multiple ages of claw marks were present (indicating seasonal revisiting); (2) broken branches occurred in the canopy (branches are broken to reach fruit), or (3) fresh claw marks coincided with fruiting in the climbed tree. Because bears also feed on fruits that have dropped to the forest floor (Fredriksson et al. 2006), the climbed trees constitute only a portion of the feeding events; as the terrestrial fruit feeding leaves no sign, I had to assume that the climbed trees were a representative sample of all feeding.

This study relied mostly on indirect evidence of bear diets. To set my observations in context, I conducted a comprehensive literature review of direct feeding evidence (scats, observations of feeding bears) for sun and black bears, augmented with field observations compiled from biologists in the region. I used this information to help interpret patterns in my data, especially where direct evidence (e.g., scats) from my study was lacking.

Resource use, abundance, and availability
Tree species composition and density.—I established vegetation plots to quantify tree species composition and density, to enable us to compare use (climbing) to availability. For MDF, I established 60 plots of 20×20 m (total 2.4 ha), each > 400 m apart, at two sites. In SEF I established one large plot (100×140 m = 1.4 ha). All trees >10 cm DBH were measured and identified. I did not establish a plot in MEF because of

its remote location. For this habitat, I used published data from a 15-ha plot in northern Thailand (Hara et al. 2002), the only data available on this forest type in Thailand. Thung Yai montane forest has a similar floristic composition to northern Thailand (van de Bult 2003).

I recorded densities of species or genera (later combined into families) that bears climbed for fruit (herein referred to as bear-trees). Densities were obtained for 84% of genera used by bears in SEF and MDF, representing all frequently-climbed families. The data set I used for MEF (Hara et al. 2002) was quantitative only at the family level, but included all MEF genera used by bears at my site. Basal area and tree density in major families were strongly correlated in each habitat (Spearman's $r > 0.78$; $P < 0.001$ in MDF, SEF; $P = 0.2$ in MEF), so I considered the density of fruiting trees a surrogate measure of food abundance.

Fruiting phenology.—I obtained two fruiting phenology data sets. First, I created a fruiting calendar by recording the months that different tree species fruited ($n = 1309$ trees), based on observations in sign transects, vegetation plots, and unrelated fieldwork. No field work was conducted in July or October in any year, so I used published phenology observations from Thung Yai for these months (Maxwell 1995). I then calculated, for each habitat, (1) numbers of tree species that fruited per month, and (2) average number of months a tree species had fruit (fruit crop persistence). Observations were made for 95% of the identified bear-tree species ($n = 79/83$) in MDF and SEF ($\bar{x} = 16.6$ trees/species). Fieldwork in MEF occurred in only 1 month so my depiction of phenology was incomplete; fruiting phenology was observed on 13/24 (54%) species climbed by bears in this habitat.

For the second data set I recorded numbers of trees with fruit (hereafter, fruiting trees) at the time of the survey ($n = 197$ fruiting trees), within sign transects and vegetation plots ($n = 71$ transects and 61 plots). These counts covered 4 rainy and 7 dry season months of the study. I calculated mean density of trees bearing fruit each month (fruiting tree density), then combined months into seasons. Fruit counts from the same season in different years were combined. Since I did not count fruiting trees every month, I may have missed some fruiting events.

Fruit nutrition.—Many fruits are high in carbohydrates, whereas lipid content varies greatly and tends to be inversely correlated with carbohydrate content (Jordano 1992). I used percent dry mass of lipids to characterize plant families as either lipid-rich (lipids >15%) or sugar-rich (lipids <15%), based on information in Van Steenis (1978), Snow (1981), Leighton & Leighton (1983), Wheelwright et al. (1984), Stiles (1993), Kitamura (2000), and Yasuda et al. (2005). Nutritional composition of fruits is strongly correlated with plant phylogeny at the genus and family levels (Herrera 2002), so these studies, though mostly from other tropical countries, are likely to reflect fruit nutrient characteristics of tree taxa in Thung Yai.

Abundance of termites.—Termite mounds were counted in some sign transects and vegetation plots (n = 13 transects in SEF, 4 in MDF, 6 in MEF; 20 MDF vegetation plots, and the SEF plot). Total area searched was 2.7 ha in MDF, 4.2 ha in SEF, and 1.8 ha in MEF. I assumed that active termite mounds represented available foods for bears.

Data analysis

I conducted quantitative analyses mainly at genus and family levels because not all climbed trees or fruit trees could be identified to species. I limited my analysis to 26 frequently-climbed families (see Results). Unidentified marks (mostly old) predominated in some genera within these families, so analysis at the genera level could not include all climbed genera. For use-abundance regressions I included those genera with trees climbed by a given bear species (black bears, n = 35 genera; sun bears, n = 44 genera). For niche breadth and overlap analyses, I included all but 3 genera with no bear-identified climbed trees (n = 49 genera).

Niche breadth and overlap.—I used Fisher exact tests to examine whether there were differences in proportions of sun bear:black bear climbing activity among tree families and genera in each habitat. I compared the selection of tree families and genera used by black and sun bears by calculating trophic niche breadths and diet overlap. I examined niche breadth with the standardized Levins's index: ($B_{standard}$): $B = \left(\sum_{i=1}^{n} p_i^2 \right)$, where n is the number of tree families (or genera) and p the proportion of records (i.e., climbed trees) in each family (or genus) i. The index was standardized as $B_{standard} = (B -$

1)/(B_{max} – 1), to produce breadths between 0 and 1. This index measures the uniformity of distribution of individuals (climbed trees) among resource categories (tree families or genera).

I estimated overlap in resource use with Pianka's index (Krebs 1999):

$$O_{jk} = \frac{\sum_i^n p_{ij}\, p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where O is the mutual overlap between bear species, p is the proportion of prey category (tree family or genus) i for bear species j and k, and n is the total number of resources. Values of O range from 0 (no resource use overlap) to 1 (complete overlap). Pianka's index is commonly used by investigators but does not account for differences in abundance among resources (Krebs 1999). I wanted to assess overlap not just between bears in each forest type, but also compare overlap indices between three forest types with disparate ranges of tree densities. Therefore, I also used Hurlbert's overlap measure (L) which accounts for resource abundance: $L = \sum_i^n \left(\frac{p_{ij} p_{ik}}{a_i} \right)$, where p is the proportion of prey category (tree family or genus) i for (bear) species j and k, and a_i is the proportional abundance of prey category i. Hurlbert's index is 1.0 when both species use each resource in proportion to its abundance, 0 when no resources are shared, and > 1.0 when certain resources are used more intensively than others and preferences of the two species tend to correspond (Krebs 1999).

Niche divergence.—I calculated selection indices for frequently-climbed tree families and genera used by each bear species, $w_i = o_i/p_i$, where w_i is the selection index for tree family(or genus) i, o_i is the proportion of family (or genus) i in the climbed tree sample, and p_i is the proportion of family/genus i available in the forest (Krebs 1999). I used this index to compare the rank order of tree selection by each bear species; if the two bear species partitioned resources, I would expect negative correlations among these indices (tested with Spearman's rank correlation).

Fruit crop size partitioning.—I examined whether bears partitioned fruit crop sizes in two ways. First, I compared mean DBH of climbed trees in each habitat, using Mann-Whitney *U*-tests. Tree DBH tends to correlate strongly with amount of fruit a tree

produces (Leighton 1993). Second, I categorized the fruit crop sizes of 60 freshly and recently-climbed fruiting trees in sign transects, as low, moderate, high, or very high, based on the density of fruits in the canopy and the proportion of the canopy with fruit (Bullock & Solis-Magallanes 1990). I used a chi-squared test to assess whether sun bears and black bears climbed trees with different crop categories. I had to combine the two highest categories to satisfy the assumption that <20% of the categories have expected frequencies <5 (Quinn & Keough 2002).

Use and abundance of bear trees—I compared tree use to abundance in two ways. First, using the complete tree data set (both bear species, all sign ages, habitats pooled), I regressed density of all climbed trees (i.e., use) on tree density (i.e., abundance). Next, using the data subset identified to bear species, I compared tree use to abundance using logit–transformed values of proportional use (% climbed) of trees as the dependent variable in a least-squares linear regression on log–transformed tree density. The logit transformation is $\ln(p_i/(1- p_i))$, where p_i is the proportion of available trees climbed in family or genus i. Species-specific analyses were conducted at both family and genera levels in each habitat. No climbed trees could be identified to bear species in Oleaceae in SEF, and Euphorbiaceae in MDF, so they were omitted from habitat-specific analyses.

I further tested whether tree family selection was influenced by (a) differential use of fruit nutrient types (lipid or sugar-rich), or (b) fruiting phenology compared to other tree families. Using my phenology calendar, I assigned families to high or low periods of fruit availability, according to whether the months that constituent species fruited tended to occur during periods when most other species also fruited. I defined high-fruit months as those with >½ the maximum monthly number of tree species that fruited in a forest type; all other months were considered low-fruit months (having ≤½ the maximum number of fruiting species for that forest type). I conducted multiple regression with these categorical predictors entered as a block following tree density. I used change in the multiple coefficient of determination ($\Delta\ r^2$) and standardized coefficients (β) to assess their contribution to the model. Data points in MEF were too few for multiple regression, so I assessed the influence of nutrients qualitatively. I report means ± SD, unless stated otherwise.

RESULTS

Diet overview

I recorded 730 bear signs, 313 (42.9%) of which were identified to species (Table 1). Signs indicated that bears mainly ate fruit. Most (85.3%) bear signs were climbed trees, 9.4% were insect-feeding signs, and the rest were scats, and debris from feeding on vegetation (Table 1). Climbed tree density in SEF and MDF, respectively, was 31.9 ± 13.5 and 10.0 ± 6.0 trees/ha, whereas density of insect feeding events/ha was 2.3 ± 4.3 and 1.7 ± 1.5. No insect feeding signs were found in MEF, and this habitat had the highest climbed tree density (37.8 ± 6.2 trees/ha).

Strong evidence of feeding (broken branches, multiple claw mark ages on a tree, fresh climbing on a fruiting tree) occurred on 70% of all within-year climbed trees ($n = 208/297$), indicating that bears climbed mostly to feed on fruits. Likewise, most scats (79%: $n = 17$ in MDF, 7 in SEF, 9 in MEF) contained fruit (Table 2). Fruits from 14 tree families were found in scats; 13 of these were also represented by freshly-climbed trees. Oaks (Fagaceae) were the most frequently observed food item in scats (FO = 18%). Insects occurred in 18% of scats. Among insects, bears ate dung beetles (Scarabaeidae) and ants (Formicidae) most. Termites were rarely eaten: none were in scats, and I found just 1opened mound (*Globitermes sulfureus*) and 1 dug nest (*Termes* sp.). Herbaceous vegetation occurred in 15% of scats (Table 1).

I recorded strong evidence of feeding on 94 plant species, in 72 genera and 42 families (Table 3, Appendix), in particular multiple climbing events on a tree. In MDF 23% of all climbed trees had been reclimbed ($n = 35$ trees), and 29% in SEF ($n = 116$ trees). Only 4% ($n = 3$) of trees in MEF had been reclimbed, although 10% of Fagaceae trees had been reclimbed.

Most (70%) of these bear-food families produce fleshy fruits, typically berries, drupes, or arillate capsules, but a few produce edible nuts (Fagaceae) or pods (Leguminosae) (Table 4). Trees in my sample from Dipterocarpaceae, which produces dry capsules that bears are not known to eat, were climbed mostly to raid stingless-bee nests. I identified only four non-tree plant families that were eaten by bears (evidence from feeding debris), corresponding to the low proportion of scats with vegetation

(Table 2): Musaceae (wild banana stem), Araceae (stem), Pandanaceae (stem, leaf base), and Palmae (rattan fruit) (Table 4).

I identified 26 families among the 3 habitat types that were climbed frequently (Table 4); I defined these as families that accounted for >2% of all climbed trees (i.e., bear species combined, all sign ages) within any one habitat. Eighty percent ($n =$ 501/623) of all climbed trees (not counting trees obviously climbed for bees) in Thung Yai were in these families. These families included 52 genera and at least 83 species that bears fed upon (Appendix). Similar genera or species from most of these same families (81%) had been reported as producing bear foods in other studies from the region (Table 4). Four frequently-climbed families in Thung Yai had not previously been reported as bear foods (Bignoniaceae, Sterculiaceae, Celestraceae, Theaceae).

Fruit and termite availability.—I identified 1676 trees >10 cm DBH in vegetation plots. Fruit-tree species used by bears accounted for 48–58% of all species and 43–53% of tree density in MDF and SEF (Table 5). The number of bear-tree species that produced fruit was highest (>20 species) during the late dry and early rainy season (April–May) in both SEF and MDF (Fig. 1). In both habitats and all but one month (Aug in MDF), at least five bear food species were in fruit.

Fruiting tree density was >10 trees/ha each month during the rainy season, and diminished by 20–50% in the dry season in each habitat (Table 5). Density of fruiting trees was highest in MEF (17.2 trees/ha), but this estimate was from only one month. Persistence of fruits on each species was about 2 months in MDF and SEF (Table 5). Persistence of acorns on individual oak trees tended to be shorter (1–2 months), but Fagaceae produced staggered acorn crops that spanned 6 months in each habitat. Lauraceae and Meliaceae species also had staggered fruiting that lasted 5–6 months in SEF.

Density of termite mounds was highest in MDF, lower in SEF, and zero in MEF (Table 5). All but 1 of 15 randomly opened mounds was active, and inhabited by *G. sulphureus* (Termitidae). However, I found only one mound excavated by a bear, indicating that this mound-building termite is not a principal food source.

Resource selection

69

Insect-feeding.—Most identifiable insect-feeding signs (27/30 = 90%), whether arboreal (stingless bees) or terrestrial (digging, log-opening), were from sun bears.

Fruit tree selection.— The number of tree climbing events (full dataset) for each family of trees was positively associated with abundance of trees in each family ($r^2 = 0.55$, $P < 0.0001$, df = 32; Fig. 2). However, the slope of this regression was <1 ($P < 0.0001$), indicating that increased abundance of each type of fruit-producing tree caused each tree of that type to be less attractive to bears. This implies that bears were selective within this suite of tree families (random use would have been implied if slope = 1).

Families (and genera) of trees that were climbed most tended to be most abundant, so the proportion of available trees that were climbed tended to be lower for common families (and genera). In SEF, both black bears and sun bears climbed Lauraceae, Meliaceae, and Fagaceae most (0.5–2.0 trees/ha; Fig. 3). Lauraceae and Meliaceae were very common (each >35 trees/ha, Fig. 3), so only a small proportion were climbed by bears (<5%). In MDF, black bears climbed Leguminosae and Dilleniaceae and (0.3 trees/ha) most, and sun bears climbed Leguminosae and Labiatae and most (0.4 trees/ha). Leguminosae was abundant (25 trees/ha), and <2% were climbed by bears. The negative relationship between proportional use and abundance of fruit-tree families was statistically significant for both bear species in SEF ($r^2 > 0.69$, $P < 0.0005$) and MDF ($r^2 > 0.3$, $P \leq 0.05$) (Table 6, Fig. 4). This relationship was even stronger for genera (Table 6). No relationship was detected between tree use and abundance in MEF, however the power of this analysis was low because of the small number of tree families ($n = 5$). However, again, the two most climbed families, Fagaceae (5 trees/ha) and Lauraceae (4.4 trees/ha), were also most common. These same relationships in each habitat also held with older marks that could not be categorized to bear species (full dataset, Fig. 3).

Nutrient type, and whether fruit was available mostly in the period of dearth or abundance, explained an additional 22–28% of variation in regression models for both bear species in MDF, but this change was not statistically significant ($B = 0.18$–0.46, $P > 0.11$). In SEF, nutrient and season were not influential ($\Delta r^2 = 0.02$ in both cases, $B = -0.04$–0.15, $P > 0.64$); tree density alone was the predominant factor influencing tree selection there.

70

Resource partitioning and overlap

I detected no differences in the ratio of black:sun bear climbing activity among tree families (Fisher exact tests, $P > 0.27$) or genera ($P > 0.44$) in any habitat. Thus, there was little evidence that one bear species was associated with particular tree taxa to the exclusion of the other species.

Family level selection indices were positively correlated in SEF ($r = 0.9$, $P < 0.0001$, $n = 14$) and MDF ($r = 0.42$, $P = 0.16$, $n = 13$). Correlations at the genus level (not shown) were weak and non-significant in SEF ($r = 0.04$, $P = 0.82$, $n = 27$) and MDF ($r = -0.16$, $P = 0.48$, $n = 22$). There were too few data to conduct similar correlations in MEF; black bear signs were predominant in MEF (Fig. 3) accounting for 83% of all identified claw marks.

Niche breadth and overlap.—Within each habitat, niche breadth of sun bears and black bears was similar (Table 7), indicating that both bear species used a broadly similar composition of tree families. Niche overlap was high in every habitat at the family level (Pianka's index >0.75), especially SEF (Table 7). At both family and genus levels, Hurlbert's overlap index was about twice as high in SEF as MDF or MEF (Table 7). This emphasized that in SEF both bear species used the same resources more intensively than others, particularly Lauraceae, Meliaceae, Fagaceae, and constituent genera such as *Lithocarpus, Quercus,* and *Beilschmiedia*. In MDF both species shared many families and genera but each was used more in proportion to its abundance.

High-fruit months were April–June in MDF, and March–June in SEF; all other months were considered low-fruit months (having ≤½ the maximum number of fruiting species for that forest type). I recalculated niche breadth and overlap indices separately for these high and low fruit periods (only genus level), to reflect breadth and overlap relative only to fruiting genera actually available in each period. Pianka's index of niche overlap increased 29% in MDF and 64% in SEF during the low fruit period (Table 7). When few tree taxa were fruiting in SEF, both bear species concentrated on the few that were, notably *Beilschmiedia*, *Magnolia*, and *Ficus*.

Do bears partition fruit-crop sizes?—Mean DBH of trees climbed by sun bears and black bears did not differ in any forest type ($P > 0.09$). Both species climbed large trees: average black bear climbed trees were 44–58 cm DBH (range of means for the three

habitats), and sun bears were 50–66 cm. Also, the two species showed no difference in selection for fruit crop rating (χ^2 = 1.62, P = 0.45, df = 2). About 70% of fruiting trees climbed by each bear species had low or moderate fruit crops, and 29–31% had abundant crops (high or very high) (Fig. 5).

DISCUSSION

Bear diets in Thung Yai

Sun bears and black bears in Thung Yai were both primarily frugivorous throughout the year; insects appeared to be of secondary importance to both species. Climbed tree density was 6–37 times higher than density of insect feeding signs. Foraging bears in North America maintain high intake rates of shrub-borne fruits by focusing on patches with the highest fruit density (Welch et al. 1997). The intensive tree climbing observed in Thung Yai might reflect a strategy where bears attempt to obtain fruits before they have been thinned by numerous arboreal competitors such as birds, squirrels, primates, and bats. Both bear species tended to climb large trees (mean DBH > 44 cm), probably because larger trees produce more fruit (Chapman et al. 1992, Leighton 1993).

Continual fruit availability sustains bear frugivory throughout the year. A minimum of four bear-tree species fruited every month (Fig. 1). In the most important food-producing families, Lauraceae, Fagaceae, and Labiatae, fruits were available for 4-6 months, due to the staggered fruiting schedules of the various species. Nonetheless, fruit crop size varies from year to year, and some or even all individuals in a species population may forgo fruiting altogether (van Schaik et al. 1993, Turner 2001). Accordingly, I observed that only about one-quarter of climbed trees had been reclimbed, suggesting that fruit production varied yearly for individual trees.

Bears fed on at least 94 plant species in 72 genera and 42 families in Thung Yai. In comparison, sun bears in Borneo fed on 113 plant species (mostly fruit trees) from 54 genera and 30 families (Fredriksson et al. 2006), the highest recorded diversity of plant foods eaten by any bear species at a single site. My study in Thung Yai documented a comparably high diversity of bear plant foods. Additionally, my study suggests that black bears are as frugivorous as sun bears. The variety of plants eaten by black bears in Thung Yai (at least 21 families; Table 4) is the highest yet observed for the species.

I could not create a definitive list of food species for each of the two bear species because I could not categorize all feeding signs to bear species. However, the congruence of feeding signs of the two bear species among the variety of taxa that were climbed (Table 4) suggests that the two species had a very similar diet. Although bears used a greater variety of fruit-tree taxa in species-rich SEF compared with MDF (Appendix), niche breadth tended to be lower in SEF (Table 7) because use was heavily concentrated within a few abundant families, especially Lauraceae, Fagaceae, and Meliaceae. These families are notable because their fruits are rich in lipids, which yield about twice the energy of other nutrients (Robbins 1993). Some species of Meliaceae and Lauraceae have high protein content (14–22 %) as well (Snow 1981). The narrower niche breadths of bears in SEF are consistent with the prediction from foraging theory that with increasing food availability, animals should concentrate more on foods that are highly profitable (Begon et al. 2006). Likewise, sun bears in Borneo fed heavily on lipid-rich fruits in Bombaceae and Burseraceae during mast fruiting events (Fredriksson et al. 2006), and Asiatic black bears in Taiwan congregated seasonally in oak habitats to eat lipid-rich acorns (Hwang et al. 2002). Acorns are especially important in diets of Asiatic black bears in temperate Asia, where they need to gain sufficient fat for hibernation (Schaller 1989, Reid et al. 1991, Huygens & Hayashi 2001, Izumiyama & Shiraishi 2004). My study showed that oaks are also heavily sought after in a tropical environment, where bears do not hibernate.

Signs of insect feeding in Thung Yai were mostly from sun bears, consistent with previous reports of this species being more insectivorous than black bears (Lekagul & McNeely 1988). But contrary to sun bear diets from elsewhere in Southeast Asia, the predominant food of sun bears in Thung Yai was fruit. In Borneo, sun bears subsist predominantly on insects throughout the year, except during mast fruiting events, when they are almost completely frugivorous (Wong et al. 2004, Fredriksson et al. 2006). The divergent diets between sun bears in Thung Yai and Borneo result from profound underlying differences in climate and tree phenology between Sundaic and mainland Southeast Asia. Most tree species in aseasonal rain-forests, such as in Borneo, fruit synchronously during mast fruiting events every 3-7 years (Primack & Corlett 2005). In contrast, the seasonal climate that prevails in mainland Southeast Asia promotes asynchronous phenology among tree species, which makes fruit consistently available throughout each year. As a result of these differences, the relative contribution

73

of insects and fruit to sun bear diets is reversed between seasonal and rain-forest ecosystems in tropical Asia.

Patterns of resource use

Use of trees by bears (climbed trees/ha) increased with abundance (trees/ha) in different families (Fig. 2), thus bears fed more on common foods than on rare foods. HoIver, tree use did not rise proportionate to abundance; in fact, the proportion of trees of each family that were climbed was inversely related to abundance, so rarer foods (e.g., Eleaocarpaceae (*Elaeocarpus* spp.) and Myrtaceae (*Syzygium* spp.)) were used at a disproportionately high rate (Fig. 4). This relationship, known as negative frequency-dependent selection (Greenwood & Elton 1979), is predicted when animals select for a mixture of complementary foods instead of focusing only on those most preferred or abundant (Leon & Tumpson 1975, Abrams 1987). Negative frequency-dependent selection has been commonly observed among herbivorous animals in both tropical and temperate settings (Owen-Smith & Novellie 1982, Dearing & Schall 1992, Skarpe et al. 2000, Edenius 2002), and is thought to occur as a result of animals seeking a mixed, nutritionally-balanced diet, or attempting to avoid or counteract dangerous levels of toxic compounds (Westoby 1978, Begon et al. 2006). This strategy is mainly relevant to generalist animals that must choose among foods that differ both in abundance and nutrition (Fryxell & Lundberg 1997).

Mixed diets also may occur as a result of variation among individual trees of the same species. Trees of the same species may produce fruit that vary from individual to individual in their nutrients, secondary compounds, or sugar content, and hence their attraction to bears (personal observation). Likewise, nearby trees of the same species may produce fruits that ripen at different rates, due, for example, to differences in penetration of sunlight through the canopy. These factors may partly explain my observations of fresh bear sign on a certain species of fruiting tree, and the absence of sign on nearby fruiting trees of the same species.

Another reason for mixed diets, broad fruit niches, and disproportionate use of rarer fruiting species in Thung Yai is simply because different fruits are available at different times. Half of the low density families in MDF (Anacardiaceae, Combretaceae) and SEF (Moraceae, Anacardiaceae, Icacinaceae) tended to fruit during the low fruit period, and thus may have attracted higher than expected use mainly because little else

was available at that time. Such taxa may function as a keystone role for bears in Thung Yai, providing fruit during periods of general scarcity. The fig family, Moraceae, is a well-known keystone resource for tropical frugivores (Terborgh 1986), including sun bears (Wong et al. 2005, Fredriksson et al. 2006). Bear niche breadths tended to widen during the annual period of fruit scarcity in Thung Yai (Table 7), consistent with the prediction from foraging theory that diets should broaden during lean seasons (Perry & Pianka 1997). Intra-annual variation in fruit availability could affect the proportion of trees climbed within families. For example, a surprisingly low proportion of Fagaceae were climbed in MDF (Fig. 4), but I do not infer that Fagaceae are not preferred— perhaps few Fagaceae trees fruited during the time covered by my sampling, so few were climbed by bears. Frequently-climbed trees were clearly selected by bears, but a longer, multi-year view of fruit availability must be considered in inferring relative preference among these taxa.

Niche overlap and coexistence
Niche overlap.—My initial three hypotheses to explain bear coexistence—that the two species of bears are complementary in their use of fruit versus insects, use different kinds of fruit, or partition fruit crop sizes—were not supported by my results. Although the two species co-occurred in two of the three major habitats (Steinmetz, Chapter 3), they both had fruit-based diets throughout the year and neither exclusively used any particular types of fruit or trees with certain fruit crops. Indeed, the two species not only selected similar fruit taxa, they also shared preferences for the same families (Lauraceae, Fagaceae, Leguminosae, and Myrtaceae). Diet similarities were manifested by generally high niche overlap indices, even (especially) during periods of diminished fruit availability. It is clear that interspecific competition for food, if operating, presently has little overall influence on diet selection by black bears and sun bears in Thung Yai, and that their coexistence is not a result of resource partitioning or niche differentiation. It is clear from the extensive diet overlap that each bear species must reduce food availability for the other, but I do not know if this reduces fitness or suppresses population density of the other species as a result; there could be weak competitive effects that I can not detect in this study.

Convergence of bear diets in Thung Yai may be largely a result of phenologic availability. Different fruit species become available for limited periods in an annual

succession; as both bear species tracked this same sequence of availability, their diets were similar. Resource tracking in seasonally fluctuating environments promotes overlapping diets among other coexisting species as well (Rotenberry 1980, Fleming et al. 1987). Although over 90 species of fruit were utilized by bears, the number available each month was much lower (Fig. 1). Additionally, nutritional variation among available fruits might further bring together the dietary choices for each species, presuming the two species have similar nutritional requirements. Whereas ecology has traditionally emphasized diet divergence between coexisting species, theoretical studies suggest that convergence in resource use can also be an adaptive response to competition, particularly for resources that are complementary, or non-substitutable, in an animal's diet. Abrams (1987, 1990) posited that depletion of non-substitutable resources by one competitor must be met with increased efforts by the other competitor to attain that resource, in order to maintain its optimal mixture of resources.

It could be argued that the perceived high dietary overlap between black bears and sun bears resulted from misclassifications of their sign. The method I used to distinguish black and sun bear claw marks, though accurate for adult animals (5% misclassification), may lead to some black bear cubs being registered as adult sun bears, resulting in inflation of the sun bear sample by as much as 8% (Steinmetz & Garshelis 2008). In SEF, most tree families (10/14) had more climbing sign from sun bears than black bears (Fig. 3), so adjusting for the possible inflation of sun bear sign would result in more equitable use (higher overlap) of these families. In MDF, conversely, I recorded more black bear sign, so increasing this to account for misclassification of black bear cubs would reduce apparent niche overlap. In MEF, the already few sun bear-sized samples, if categorized instead as black bear cubs, would strengthen my conclusion that this habitat was dominated by black bears. I also wondered if unidentified claw marks, which were mostly old (73%), might have presented a different picture of tree use overlap by bear species than I observed with identifiable marks. Proportions of climbed trees with and without identifiable marks were similar among tree families in each forest type ($\chi^2 < 14$, $P > 0.43$), so the probability of finding identifiable claw marks seemed little affected by differences between habitats or tree characteristics. Therefore, I believe the bear-identified subsample was likely representative of most climbed trees.

Coexistence.—The broad food niches and extensive ecological overlap of sun bears and black bears indicates the potential for intense competition, if food is a limiting resource. Yet, these species have co-occurred in mainland Southeast Asia since at least the Middle Pleistocene and neither competitive exclusion nor obvious niche divergence has occurred. I propose three mechanisms that may have led to this situation: (1) resource abundance, (2) negative density-dependent selection, and (3) exclusive use of some resources.

Resource abundance. Extensive niche overlap between species may reflect an abundance of food (Sale 1974, Wiens 1993); two species may thus share resources without really competing (Smith & Smith 2001). Fruit resources in Thung Yai were diverse and abundant, and may not be limiting for bears, especially given that bears in this area were once heavily hunted and were probably still recovering at the time of my study. Density of bear-trees in Thung Yai was about twice as high as a site on Borneo inhabited by sun bears (Fredriksson et al. 2007), yet these sun bears had very small home ranges, indicative of plentiful food. Moreover, fruit in Thung Yai was consistently available, season to season and year to year; mean monthly fruiting tree density did not drop below 6 trees/ha.

Negative frequency dependent resource selection. As bears of one species increase the diversity of fruits consumed, they consequently consume less of each type of fruit, providing a potential surplus of common fruits for the other species. For example, sun bears climbed only 4% (2 trees/ha) of available Lauraceae trees (Fig. 3), leaving potentially 45 trees/ha as food for black bears.

Exclusive use of resources. I found that each species used one resource nearly exclusively: sun bears were the main consumer of insects, and black bears predominated in fruit-rich montane forest. If different species have some exclusive resources in addition to shared ones, then a certain density of each species can be maintained that is unaffected by competition from the other species, generating conditions for coexistence (Ritchie 2002). It is plausible that the near-exclusive use of insects and MEF by sun bears and black bears, respectively, promotes their coexistence in Thung Yai despite widely overlapping diets and shared preferences for fruit in SEF and MDF. This mechanism appears to promote coexistence of sympatric carnivores that share similar overall diets in other areas (Kitchener et al. 1999, Neale & Sacks 2001, Azevedo et al. 2005).

77

MEF differs from SEF and MDF in two respects that might lead to competitive exclusion of sun bears. First, ants, termites, and bees, which supplement the diet of sun bears in SEF and MDF, were scarce in MEF, and I observed no insect feeding signs there. Biomass and richness of ants and termites diminishes with increasing elevation in the tropics (Collins 1989, Phoonjampa 2002), reaching zero towards 1900 m (Collins 1980). Second, favored fruit tree families Lauraceae and Fagaceae are especially abundant in MEF, with combined density (138 trees/ha; Hara et al. 2002) twice as high as in SEF (61 trees/ha; this study, Fig. 3). This could impede bear species coexistence because interference competition becomes intensified where preferred foods are concentrated in space. In North America, for example, larger grizzly bears dominate rich food patches such as salmon streams and moth aggregations, and smaller American black bears avoid these areas as a result (Mattson et al. 1991, Aune 1994, Jacoby et al. 1999, Belant et al. 2006). Black bears climbed 7% of available Fagaceae and Lauraceae in MEF, compared with just 3% of these families in SEF, suggesting a higher black bear density in MEF. The concentration of preferred fruit trees in MEF in Thung Yai, combined with the prevalence of Asiatic black bears there, might make it difficult for the smaller-sized sun bears to exploit this rich habitat without encountering a black bear.

Table 1. Signs of sun bears and Asiatic black bears (species combined, all sign ages) recorded in sign transects (n = 71) in Thung Yai Naresuan Wildlife Sanctuary, Thailand, 2001–2003.

Sign category	Indicative of feeding on:	Number of signs	% of total	Bear species identified	
				N	% of category
Climbed trees	Fruit	623	85.3	279	44.6
Raided stingless bee nests[1]	Stingless bees	25	3.4	10	40.0
Broken logs; holes dug[2]	Insects	44	6.0	20	44.5
Feeding debris	Vegetation	5	0.7	4	80.0
Scat	Various	33	4.5	0	0.0
Total		730	100	313	42.9

[1]These are usually also on climbed trees. [2]Includes signs recorded opportunistically off transects.

Table 2. Frequency of occurrence (% FO) of food items identified in scats ($n = 33$) of sun bears and Asiatic black bears collected in Thung Yai Naresuan Wildlife Sanctuary, 2001–2003.

Category	Family	Species name(s)	% FO
Fruit	Fagaceae	*Quercus semiserrata*	18.2
	Moraceae	*Ficus* sp.	12.1
	Ebenaceae	*Diospyros glandulosa*	12.1
	Leguminosae	*Cassia fistula, Dalbergia* sp.	9.1
	Euphorbiaceae	*Antidesma, Baccaurea ramiflora*	6.1
	Rubiaceae	*Adina diversifolia*	6.1
	unidentified		3.0
	Lauraceae	*Cinnamomum* sp. *or Phoebe* sp.	3.0
	Anacardiaceae	*Rhus chinensis*	3.0
	Sapotaceae	unidentified	3.0
	Flacourtiaceae	*Casearia mekongii*	3.0
	Symplocaceae	*Symplocos sumnita*	3.0
	Rhamnaceae	*Ziziphus rugosa*	3.0
	Icacinaceae	*Apodytes dimidiata*	3.0
	Meliaceae	*Aglaia* sp.	3.0
Insects	Scarabaeidae		9.1
	Formicidae	*Cerebera* sp., *Camponotus* sp., *Tetraponera ruflonigra*	6.1
	Polydesmidae		3.0
	Cicinellidae		3.0
	Vespidae		3.0
Vegetation	herbaceous	unidentified	12.1
	Araceae (stem)	*Alocasia* sp.	3.0
	Musaceae (stem)	*Musa* sp.	3.0
	flower bud	unidentified	3.0

Table 3. Distribution of different types of bear feeding evidence (sun and black bears combined) among plant taxa in ThungYai Naresuan Wildlife Sanctuary, Thailand, 2001–2003.

| Plant taxa | Climbed trees ($n = 208$) | | | Scat $n = 33$ | Feeding debris $n = 5$ | Total (cumulative) plant taxa with feeding evidence |
	Broken branches	Multiple climbing events on a tree	Fresh marks on fruiting tree			
Families	6	33	23	14	4	42
Genera	6	57	30	16	4	72
Species	10	77	40	16	4	94

Table 4. Plant families with evidence of feeding by sun bears and black bears in Thung Yai Naresuan Wildlife Sanctuary, Thailand (2001–2003), cross-referenced with observations from elsewhere in Asia. Evidence from this study (bold number 16) includes scat, feeding debris, and feeding signs on climbed trees (see Appendix for details). Families in bold font were frequently-climbed in Thung Yai (>2% of records). Nutrient type indicates whether fruits are lipid-rich or sugar-rich (see text). Obs. = direct observation of a bear feeding; branch = broken branches from feeding; Bear sp. = feeding evidence not distinguished to species; n/a = not applicable.

Plant family	Fruit type	Nutrient type	Part eaten (other studies)	Feeding evidence (other studies)	Smyce of evidence		
					Sun bear	Black bear	Bear sp.
Anacardiaceae	drupe	lipid	fruit	scat, obs.	3, **16**	7, **16**	
Annonaceae	berry	lipid	fruit	scat, obs.	3, 5, 9		**16**
Apocynaceae	follicle	sugar	fruit	scat, obs.	3 (liana),**16**		**16**
Araceae	n/a	no data	shoot	scat, obs.	**16**		26
Araliaceae	berry	no data	fruit	none		17	**16**
Bignoniaceae	capsule	no data	unknown	none	**16**	**16**	
Burseraceae	drupe	lipid	fruit	scat, obs.	5, 9, 3		19
Celestraceae	aril	sugar	unknown	none	**16**	**16**	
Combretaceae	drupe	sugar	fruit, leaf, flower	scat, obs.	**16**	**16**	4[1]
Dilleniaceae	aril	sugar	Fruit	obs.	9, **16**	24, **16**	
Dipterocarpaceae	n/a	n/a	nesting bees[2]	raided nests[2]			**16**
Ebenaceae	berry	sugar	Fruit	scat, obs.	3	7, 13, 27	**16**,18,26
Eleaocarpaceae	drupe	sugar	Fruit	scat		**16**	6[1]
Euphorbiaceae	drupe, berry	sugar	Fruit	scat, obs.	3, 9, **16**	7	**16**, 18
Fagaceae	nut	lipid	Nuts	scat, obs.	3, 9, **16**	1,7,2,8,12,13,**16**	**16**, 26
Flacourtiaceae	berry	sugar	Fruit	scat		**16**	**16**
Guttiferae	berry	sugar	Fruit	scat, obs.	3, **16**		
Icacinaceae	drupe	lipid	Fruit	scat, obs.	21, **16**	21	**16**, 26
Juglandaceae	samara	no data	unknown	none		**16**	
Labiatae	drupe	sugar	Fruit	scat, obs.	**16**	**16**, 23	
Lauraceae	berry	lipid	Fruit	scat, obs.	3, 9, **16**	7, 10,12,13, **16**	**16**,18,26
Lecythidaceae	berry	no data	flower	obs.	3	**16**	
Leguminosae	pod	lipid	Fruit	scat, obs.	3, **16**	**16**, 26, 8	**16**, 14[1]
Lythraceae	capsule	no data	unknown	none	**16**		
Magnoliaceae	aril	lipid	fruit, flower, bark	obs., scat	3, **16**	15, 20, **16**	
Meliaceae	aril	lipid	fruit	scat	3, 9, **16**	20, **16**	**16**
Moraceae	berry	sugar	fruit	scat, obs.	3, 5, 9, **16**	7, **16**	**16**
Musaceae	n/a	n/a	shoot	obs.			**16**
Myristicaceae	aril	lipid	fruit	scat, obs.	3, 9, **16**		
Myrtaceae	berry	sugar	fruit	scat, obs.	3, 9, **16**	**16**	18, 14[1]
Oleaceae	drupe	lipid	fruit	branch		25	**16**
Palmae	drupe	sugar	fruit, shoot	obs.	3, **16**	**16**	
Pandanaceae	compound	n/a	shoot	obs.	3, **16**		
Rhamnaceae	drupe	sugar	fruit	scat		17	**16**

Rosaceae	drupe	sugar	fruit	scat, obs.	22, **16**	7, 2, 11, **16**	
Rubiaceae	compound	sugar	fruit	scat	**16**		**16**
Sapindaceae	aril	sugar	fruit	scat, obs.	3, 9, **16**	7, **16**	26
Sapotaceae	berry	sugar	fruit	scat	3		**16,** 26
Sterculiaceae	follicle	lipid	unknown	none			**16**
Symplocaceae	drupe	sugar	fruit	scat		1	19,**16**,26
Theaceae	berry	sugar	unknown	none		**16**	
Tiliaceae	berry	sugar	fruit	scat, obs.	3, **16**	**16**	18, 14[1]

Sources: (1) Sathyakumar & Viswanath 2003, (2) Manjrekar 1989, (3) Fredriksson at al. 2006, (4) Chhangani 2002, (5) McConkey & Galetti 1997, (6) Sreekumar & Balakrishnan 2001, (7) Hwang et al. 2002, (8) Saberwal 1989, (9) Wong et al. 2002, (10) Kitamura 2000, (11) Huygens & Hayashi 2001, (12) Reid et al. 1991, (13) Schaller et al. 1989, (14) Joshi et al. 1997, (15) Nozaki et al. 1983, (16) this study, (17) Corlett 1998, (18) Kitamura et al. 2002, (19) Kitamura et al. 2005, (20) Takahashi et al. 2007, (21–27) personal comm. with, respectively: Prawing, W. Sangkametale, Loong Nong, Mon Tu-U, Naim Ahktar, D. Ngoprasert, R. Phoonjampa. [1]Data for sloth bear (*Melursus ursinus*), included for comparison. [2]Feeding evidence from this study only.

Table 5. Attributes of forest structure and bear food availability in three habitats of Thung Yai Naresuan Wildlife Sanctuary, 2001–2003. The first five attributes were measured in vegetation plots (Semi-evergreen, 1.4 ha; Mixed deciduous, 2.4 ha; Montane evergreen, 15 ha [from Hara et al. 2002]); remaining attributes were measured in vegetation plots plus sign transects.

Habitat attribute	Semi-evergreen	Mixed deciduous	Montane evergreen
Total tree density (trees > 10 cm/ha)	559	373	519[1]
Basal area (m^2/ha)	42.8	25.8	40.0[1]
Bear-food species richness[2] (% of total species in plots)	61/105 (58%)	70/147 (48%)	29/165[1] (18%)
Bear-food genera richness[2] (% of total genera in plots)	41/50 (82%)	58/118 (49%)	28/106[1] (26%)
Bear food-tree density (% of total density in plots)	239 (43%)	197 (53%)	221[1] (43%)
Mean fruiting tree density/month – Rainy season	10.9 ± 2.8	13.4 ± 12.3	no data
Mean fruiting tree density/month – Dry season	8.0 ± 5.6	6.4 ± 5.5	17.2
Mean fruit persistence per species (months)	2.2 ± 1.2	2.5 ± 1.2	no data
Termite mound density	1.2 ± 1.7	5.3 ± 10.3	0.0

[1]Data from Hara et al. (2002). [2]Plot sizes were different so species richness values not strictly comparable.

Table 6. Results of linear regression analysis of proportion of trees climbed by bears (logit-transformed), on available tree density (log-transformed) in three forest types, Thung Yai Naresuan Wildlife Sanctuary, 2001–2003. Data points (*N*) are numbers of frequently-climbed families and genera.

Forest type, model and parameter estimates	Tree Families		Tree Genera	
	Black bears	Sun bears	Black bears	Sun bears
Semi-evergreen Forest				
N	14	14	17	24
F	26.6	43.96	71.51	49.44
r^2	0.69	0.79	0.83	0.69
P	< 0.0005	< 0.0001	< 0.0001	< 0.0001
Intercept	−1.76	−1.30	−1.88	−2.11
Slope ± 95% CIs	−0.89 ± −0.37	−0.82 ± −0.27	−1.0 ± −0.25	−0.65 ± −0.19
Standardized coefficient (*B*)	−0.83	−0.89	−0.91	−0.83
Mixed Deciduous Forest				
N	13	13	18	20
F	4.75	6.97	32.31	51.1
r^2	0.30	0.38	0.67	0.74
P	0.05	0.02	< 0.0001	< 0.0001
Intercept	−3.07	−2.42	−2.71	−2.52
Slope ± 95% CIs	−0.61 ± −0.60	−0.83 ± −0.69	−0.84 ± −0.31	−0.89 ± −0.26
Standardized coefficient (*B*)	−0.55	−0.62	−0.82	−0.86
Montane Evergreen Forest				
N	5	5	*not assessed*	*not assessed*
F	0.17	2.63		
r^2	0.05	0.35		
P	0.71	0.25		

Table 7. Indices of niche breadth (Levins's standardized) and overlap for sun bears and Asiatic black bears using frequently-climbed fruit-tree families and genera in three forest types, Thung Yai Naresuan Wildlife Sanctuary, 2001–2003. Genera indices were calculated separately for annual high and low fruit availability periods.

Taxonomic resolution	Forest type	Niche breadth		Niche overlap	
		Black bear	Sun bear	Pianka's index	Hurlbert's Index
Families	Semi-evergreen	0.50	0.49	0.91	2.10
	Mixed deciduous	0.61	0.64	0.75	1.21
	Montane evergreen	0.59	0.64	0.78	0.79
Genera	Semi-evergreen				
	high-fruit period	0.51	0.45	0.57	1.73
	low-fruit period	0.58	0.71	0.94	1.72
	Mixed deciduous				
	high-fruit period	0.49	0.70	0.58	0.98
	low-fruit period	0.74	0.50	0.75	1.12

Figure 1. Numbers of fruit-tree species used by bears with fruit each month in semi-evergreen forest (SEF) and mixed deciduous forest (MDF), Thung Yai Naresuan Wildlife Sanctuary, Thailand (2001–2003).
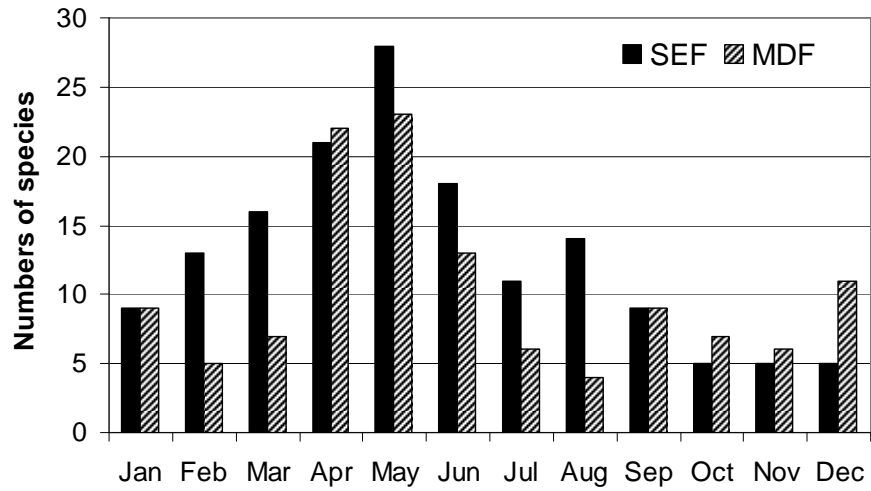
Figure 2. Trees climbed by sun bears and black bears (combined), as a function of tree density among frequently-climbed families across three habitats (up to 3 points per family) in Thung Yai, Thailand, 2001-2003.

$Y = -0.7 + 0.04 \, (X)$
$r^2 = 0.55, \, P < 0.0001$
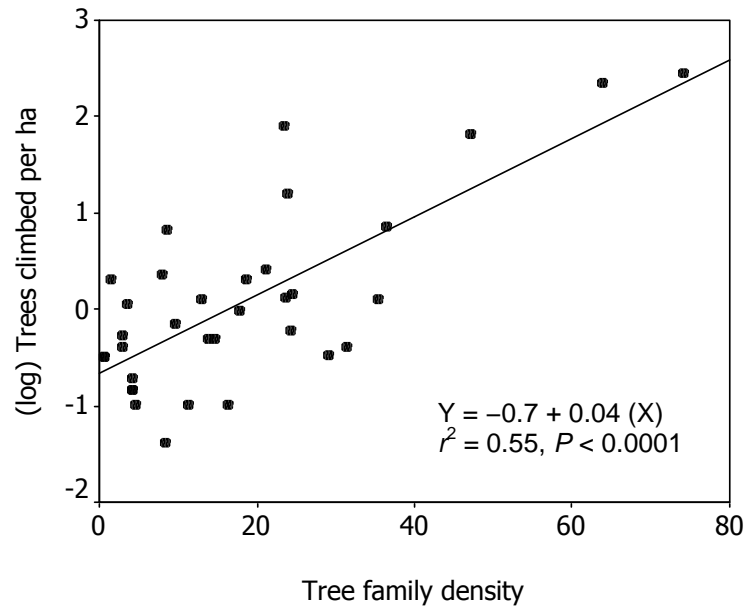
Figure 3. Abundance and use of frequently-climbed tree families by sun bears and black bears in three forest types in Thung Yai Wildlife Sanctuary, 2001–2003 (arranged by increasing sun bear use). Bears were identified from claw marks on climbed trees. 'Bear sp.' represents marks not identified to species. Inset shows available tree density in the forest, with families arranged in same order as main graph.
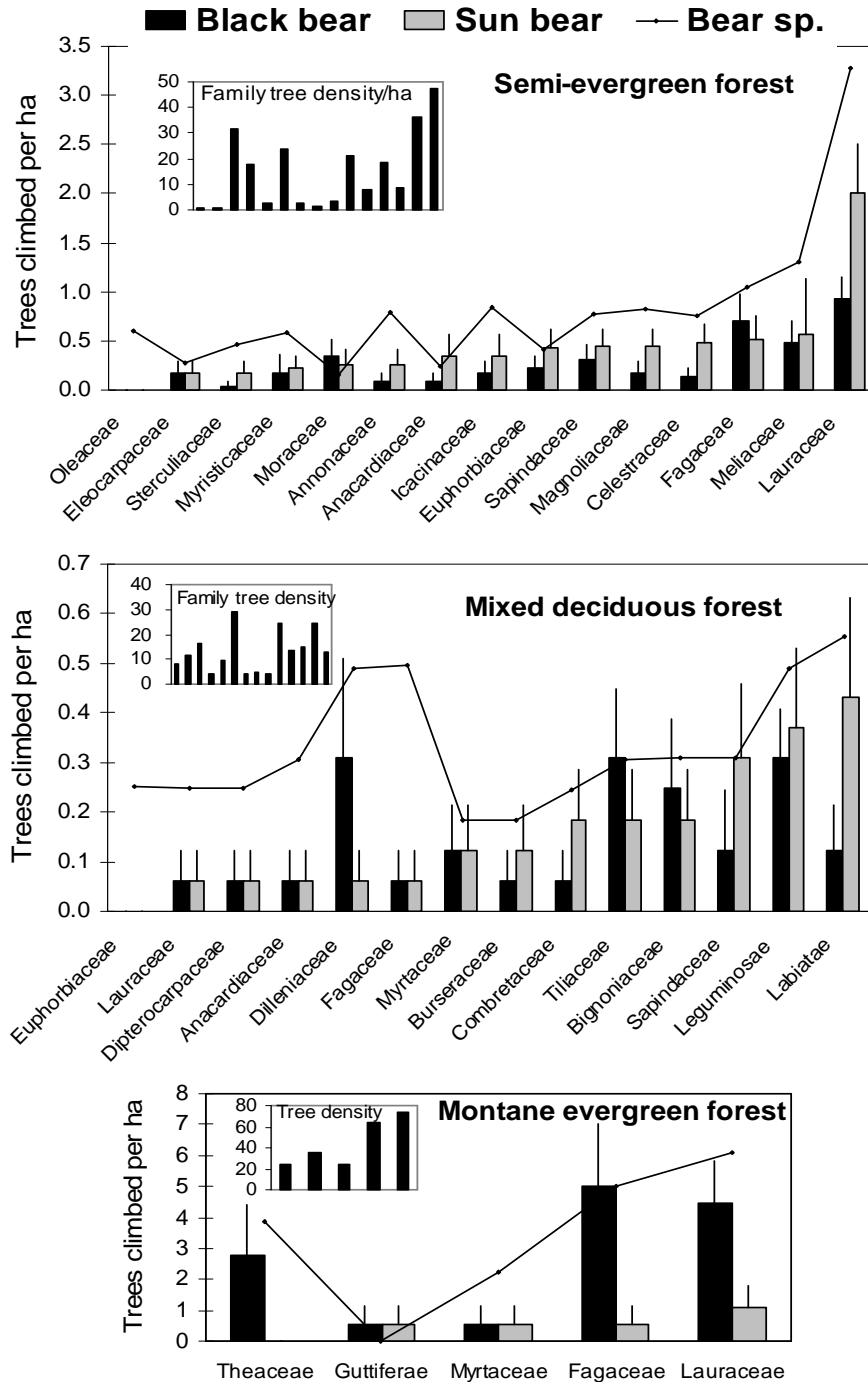
Figure 4.   Linear regressions of tree abundance and proportional use of frequently-climbed tree families, by sun bears and black bears in Thung Yai Naresuan Wildlife Sanctuary, 2001–2003. Abbreviations are first four letters of family name (see Table 4 for full name). Typical nutrient type of fruits in each family designated as (L) lipid-rich, or (S) sugar-rich.
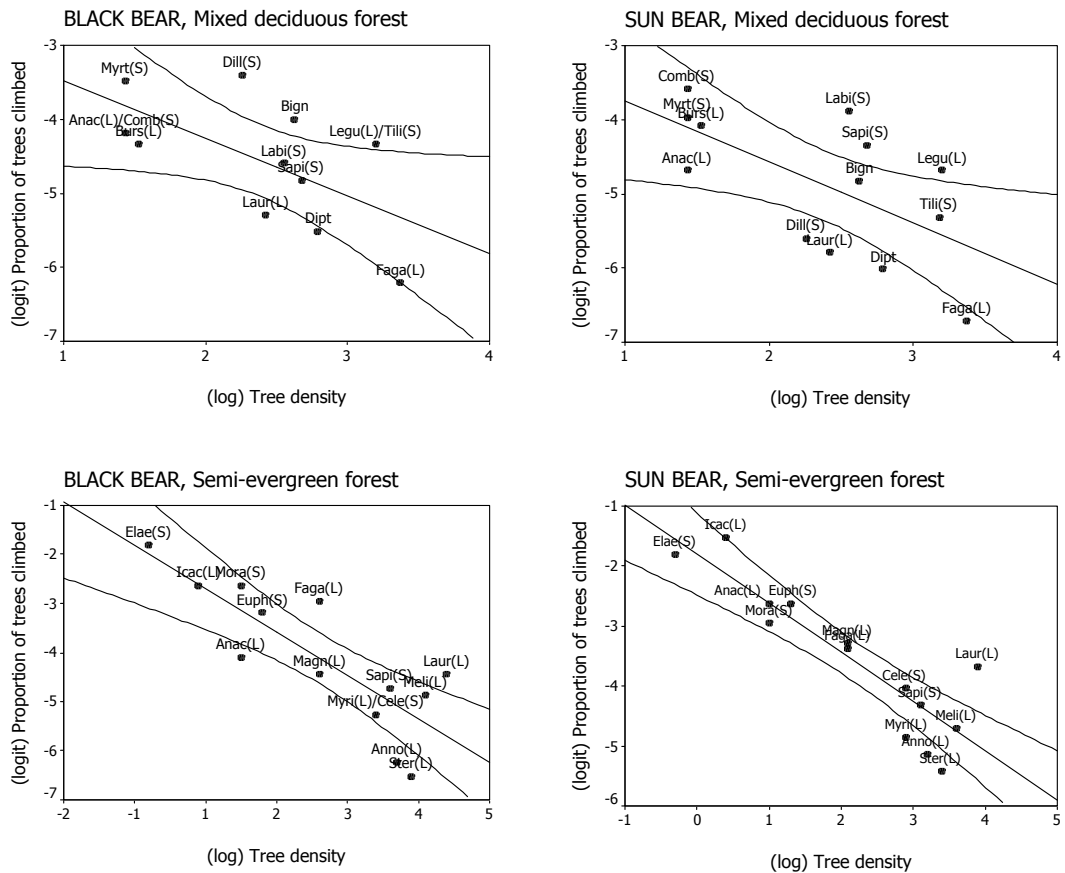
Figure 5. Percent of fruiting trees (n = 60) with different fruit crop sizes (low to very high) that were climbed by bears in Thung Yai Naresuan Wildlife Sanctuary, 2001–2003.
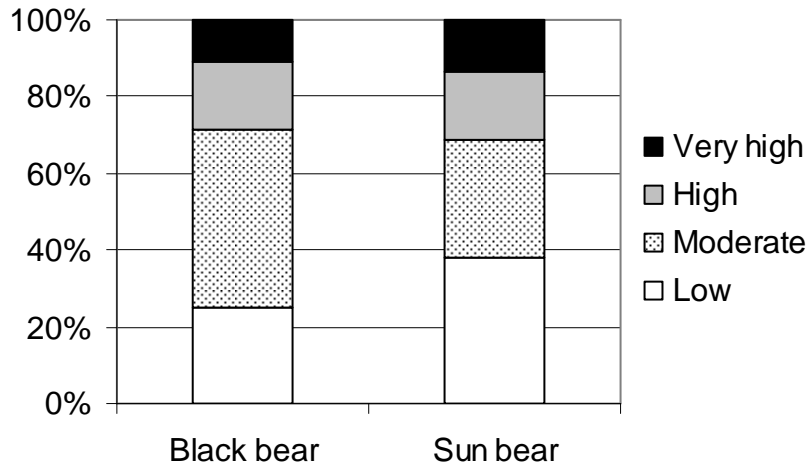
Epilogue: Conservation implications of bear sign surveys

Mapping distribution

In 2005, IUCN's Bear Specialist Group (BSG) identified priorities for bear conservation in Asia (see Garshelis & Steinmetz 2005). The top priority identified by most countries was to map the extant distribution of each bear species. The rationale for this priority was that it was impossible to plan for bear conservation when even bear presence in different areas was unknown.

At the same time, the Department of National Parks, Wildlife, and Plant Conservation (DNP) in Thailand initiated a national survey of the distribution of large mammals throughout the country's protected area system, based on incidence of sign. Thus, the opportunity arose to act on the BSGs recommendation. When the DNP learned of the claw mark method I was developing, they requested training in order to apply it in their upcoming field surveys. Had this method not been available, they could only have recorded "bear sp." in the field. Training was conducted, the survey proceeded, and one result was the first reliable map of the two species of bears in Thailand (Vinitpornsawan et al. 2006).

This sign survey also produced five important discoveries about sun bears and black bears in Thailand. First, both species were still widely distributed throughout the country, occurring in 64% and 53% of protected areas, respectively (Vinitpornsawan et al. 2006). Second, both species co-occurred in most surveyed areas, confirming that the coexistence documented for Thung Yai (Chapters 3, 4) is a widespread pattern. Third, bear sign was documented in 10 different habitat types, from montane evergreen forest to secondary growth after agriculture, emphasizing that each species is indeed a habitat generalist, as suggested by the habitat modeling in Chapter 3. Fourth, five key forest complexes were identified, in which populations were most secure, and across which different ecological regions (from north to south) were represented. Fifth, the southern boundary of the geographic distribution of black bears in Southeast Asia,

heretofore unknown, was documented; it occurs at Tai Rom Yen National Park, at about 11°N latitude, midway down the Thai peninsula.

The sign-based techniques that enabled bear mapping in Thailand have attracted interest from other countries in Asia. Recently, at the request of conservation NGOs (non-government organizations) in Cambodia and Bangladesh, protected area officials and rangers from throughout these countries were trained in bear sign survey methods (Steinmetz et al. 2007, La Combe 2008). With these tools in place, bear sign surveys have since been initiated in both countries, leading to better knowledge of the status of each species. In Bangladesh, for example, it has been learned that sun bears are very rare, possibly because they are less well adapted to small, heavily-degraded forest patches with high human use.

Monitoring habitat use and population abundance

Animal density can be determined from estimates of the rate at which their sign is produced and decays. This technique has been used to estimate the density of animals such as great apes, elephants and deer, which are difficult to directly observe and count. However, imprecision in estimates of the rate of sign production and decay may result in unreliable estimates of abundance. Studies have employed varied approaches to the estimation of sign decay rates (e.g., Laing et al. 2003, Kuehl et al. 2007); likewise, I was able to estimate bear sign (claw-mark) decay rates in this study (Chapter 2). These results could be further extended to estimate rates of sign production, by physically marking (e.g., by slashing with a knife) fresh claw marks in an area (analogous to wiping the area clean of marks), then returning and counting new fresh marks in the same area that accumulated over the inter-visit interval. To convert this to an estimate of density, however, would require an estimate of the number of marks created per bear, which would be an elusive parameter to estimate (requiring either bears that are easily observable [e.g., Fredriksson et al. 2006], or an area with a known number of bears).

Instead, the sign age criteria and decay rates are probably most applicable for monitoring population change. For example, sign samples increasingly dominated by older signs might indicate a declining population, whereas an area recovering from hunting should show increasing proportions of fresh sign. Even this application, though, may be problematic, if per-animal sign production rates vary with varying availability of

food. Year-to-year variability in fruit production can be large in parts of Southeast Asia (Wong et al. 2005): low average fruit production per tree could force bears to climb more trees/day, or could prompt more feeding on insects and vegetation and hence less tree climbing (Fredriksson et al. 2007); moreover, rates of tree climbing may vary with differing types of fruits being common in different years (Fredriksson et al. 2006). To monitor a population, it would be necessary to make the (reasonable) assumption that, over an extended period of time, rates of sign production and decay remain fairly constant. A difficulty yet to be worked out, is how to deal with shifts in bear distribution to different habitats, where rates of sign production may be different.

Relative abundance of black bears and sun bears

This study enables one to potentially evaluate and monitor the relative abundance of sun bears and black bears, based on the reasonable assumption that sign abundance is related to bear abundance. However, sign density also reflects bear activity and behavior, so inferences regarding relative abundance should be made cautiously, and in light of concurrent information regarding food availability. It may be that the two species of bears exhibit different foraging strategies even though their diet is very similar: average number of trees climbed per day may differ between the two species, and this difference may vary with food conditions. For example, sun bears might be relatively more arboreal than black bears (Lekagul & McNeely 1988), so might produce more climbed tree signs irrespective of density. Conversely, larger black bears might be expected to have more broadly distributed sign due to larger ranges, and individuals might produce more sign per unit area because they (presumably) eat more. Despite these considerations, it seems likely that sign abundance should broadly reflect the abundance of each species, because both species have similar foraging behavior and track the same seasonal sequences of fruit availability (Chapters 3, 4).

Sun bears produced more signs/ha in lowland forests (semi-evergreen and mixed deciduous) in Thung Yai (Chapter 3), suggesting somewhat higher sun bear abundance in those habitats. This interpretation corresponds to camera trap data from 24 sites in Southeast Asia, including Thung Yai, in which sun bears were the more commonly photographed species at lower elevations (R. Steinmetz, unpub. data). In contrast, in Thung Yai's montane forest, black bears produced more signs/ha (Chapter

94

3); correspondingly, black bear tended to be the more commonly photographed species at higher elevations in recent camera trap studies (R. Steinmetz, unpub. data).

The apparent lower abundance of black bears in Thung Yai (except in remote montane forest) and more generally in the region may reflect differential effects of the long-standing commercial trade in bear parts in Asia. Asiatic black bear is the most valued bear species in traditional Chinese medicine (Servheen 2001), and there is a vigorous international trade in bear parts (paws, gall bladders, canines) in Southeast Asia that preferentially targets black bears (Shepherd & Nijman 2008). Montane regions may serve as refugia for black bears since these areas are less accessible to hunters (Steinmetz et al. 2008); however, montane regions in Southeast Asia encompass much less physical area than lowlands (Stibig & Beuchle 2003), so will collectively support fewer bears.

Why are bears faring better than tigers in hunted habitat fragments?
Commercial poaching of bears for the wildlife trade is a considerable threat in most countries in Southeast Asia (Nea & Nong 2006, Nguyen Xuan Dang 2006, Saw Htun 2006, Tumbelaka & Fredriksson 2006, Wong 2006), and is the main threat where deforestation is currently negligible (for example in Thailand where nearly all remaining forest is protected). Killing bears is illegal in all range countries but is largely uncontrolled. In Thailand, local hunters in one area estimated that commercial poaching reduced the abundance of sun bears by 50% in 20 years (Steinmetz et al. 2006).

Despite significant poaching, bear populations appear to persist longer in forest patches of Southeast Asia than some other heavily-exploited large carnivores. For example, tiger (*Panthera tigris*) populations have been severely reduced or extirpated in 12 of 15 protected areas surveyed in Myanmar, but sun bears were still encountered relatively frequently in 13 of these areas (Lynam 2003, Saw Htun 2006). Similarly, in Thailand tigers are close to extirpation in the Khao Yai forest complex, but sun bears and black bears persist (Lynam et al. 2006, Vinitpornsawan et al. 2006) and indeed still use most of the park and are regularly seen by visitors (D. Ngoprasert, pers. comm.).

Bears and tigers both have high value body parts that are intensively sought by commercial poachers. Bear and tiger body parts are similarly used in Chinese medicine and destined for the same markets. And both bears and tigers suffer from habitat loss and fragmentation that exacerbates the effects of hunting. Why, then, have bears fared

better than tigers? I offer two explanations. First, because tigers are territorial whereas bear home ranges broadly overlap, a given area will naturally hold a smaller—and thus more easily extirpated—population of tigers than bears. Second, tiger food supply is more limiting. This study showed that sun bears and black bears rely mainly on wild fruit and insects (Chapters 3, 4), for which there is little competition from humans. In contrast, tigers rely mainly on ungulate prey, which in Southeast Asia is also heavily exploited by humans, resulting in severely reduced populations and many local extirpations (Sanderson et al. 2006). Prey depletion, combined with direct poaching, likely contributes to the more critical status of tigers compared with either species of bear.

Ecology of recolonization

The process of species extinction entails the loss of animal populations as habitat patches are eroded, degraded, or hunted out. Reversing this process can involve maintaining or creating connections between forest areas to enhance persistence through recolonization. Understanding the ecology of recolonization processes could enable conservation biologists to manage habitat in ways that encourage recolonization of empty or sparsely-populated forests.

In 2002, black bear(s) unexpectedly appeared in a small 10 km^2 patch of 12-year secondary forest adjacent to Khao Yai National Park, Thailand (R. Steinmetz, unpub. data). Signs, mostly claw marks on climbed trees, indicated that the colonizers were black bears; this was later confirmed by camera traps set by a local NGO that protected and monitored the site. Claw-marked trees indicated that the bears fed on fruits from common secondary tree species particularly *Ficus hispida* and *Gmelina arborea* (R. Steinmetz, unpub. data). Black bears appear to have permanently occupied the site, as fresh signs and sightings have been consistently recorded to the present.

This example illustrates the ecological adaptability of Asiatic black bears, and reveals their ability to survive in secondary scrub forest of low plant diversity. Regenerating secondary forests are more common than undisturbed forests; that black bears can recolonize and persist in such a habitat bodes well for their population recovery.

These observations expand our knowledge of black bear ecology, but an unanswered question is whether sun bears could also live alongside black bears in

such secondary forest. In particular, is there enough food and space to support both species, and are sun bears attracted to such habitat? Sign surveys in other parts of their range (where black bears are absent) suggest that sun bears are less inclined to use young, secondary forests (Augeri 2005). Improved understanding of factors governing coexistence such as this are needed to address the conservation of natural communities (Holt 2001).

Maintaining and recovering bear populations

Reducing the trade in bear parts is crucial to the survival of sun bears and black bears in Southeast Asia. However, given available resources, the necessary patrolling and monitoring of entire protected areas is an overwhelming task. To make this problem more manageable, a network of small bear recovery zones (100–200 km^2) could be established within key protected areas, and patrolling efforts of rangers could be focused on these zones.

Information on important bear foods and their phenology gathered during this study could be used to select the location of such recovery zones. Zones should be forest types or patches with plentiful bear food-producing trees from important families such as Lauraceae, Moraceae, Burseraceae, Myrtaceae and Fagaceae. Places with a diversity of species that provide fruit at different times of year would be more apt to contain bears that are year-round residents. Such zones would provide a biologically meaningful, geographically focused, and logistically realistic way for the efforts of protected area staff to be translated into population recovery for bears (and other wildlife species).

Recently, the Bear Specialist Group mapped the current, range-wide distribution of sun bears and black bears. Important habitat blocks for long-term survival were identified (Bear Conservation Units-BCUs). Anti-poaching efforts within these BCUs should be a high priority. Trends in bear occurrence and relative abundance within BCUs could be monitored using standardized sign surveys and camera trapping. Results of such monitoring could indicate which management or ecological conditions promote successful bear conservation, and which do not, and provide a means of assessing the results of conservation efforts (e.g., future range expansion and/or increased bear density being indicative of effective conservation efforts).

BIBLIOGRAPHY

Abrams, P. 1987. Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. Evolution 41: 651-661.

Abrams, P.A. 1990. Mixed responses to resource densities and their implications for character displacement. Evolutionary Ecology 4: 93-102.

Alexander, S. M., T. B. Logan, and P. C. Paquet. 2006. Spatio-temporal co-occurrence of cougars (*Felis concolor*), wolves (*Canis lupus*) and their prey during winter: a comparison of two analytical methods. Journal of Biogeography 33: 2001-2012.

Apps, C. D., B. N. McLellan, and J. G. Woods. 2006. Landscape partitioning and spatial inferences of competition between black and grizzly bears. Ecography 29: 561-572.

Augeri, D.M. 2005. On the biogeographic ecology of the Malayan sun bear. PhD. Thesis, Cambridge University, Cambridge, U.K.

Aune, K. E. 1994. Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana. International Conference for Bear Research and Management 9: 365-374.

Azevedo, F.C.C., V. Lester, W. Gorsuch, S. Lariviere, A.J. Wirsing, and D.L. Murray. 2006. Dietary breadth and overlap among five sympatric prairie carnivores. Journal of Zoology 269: 127-135.

Basset, A. and D.L. Angelis. 2007. Body size mediated coexistence of consumers competing for resources In space. Oikos 116: 1363-1377.

Begon, M. C.R. Townshend, and J.L. Harper. 2006. Ecology: from individuals to ecosystems (4th ed.). Blackwell Publishing, Malden, Massachusetts.

Belant, J. L., K. Kielland, E. H. Follmann, and L. G. Adams. 2006. Interspecific resource partitioning in sympatric ursids. Ecological Applications 16: 2333-2343.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12: 244-257.

Brodie, J.F. 2006. An experimentally determined persistence-rate correction factor for scat-based abundance indices. Wildlife Society Bulletin 34: 1216-1219.

Brown, J.S., B.P. Kotler, and W.A. Mitchell. 1994. Foraging theory, patch use, and the structure of a Negev Desert granivore community. Ecology 75: 2286-2300.

Bunyavejchewin, S., P. J. Baker, J. V. LaFrankie, and P. Ashton. 2002. Floristic composition of a seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, western Thailand. Natural History Bulletin of the Siam Society 50: 125-134.

Buskirk, S. W., and J. J. Millspaugh. 2006. Metrics for studies of resource selection. Journal of Wildlife Management 70: 358-366.

Carbone, C., G.M. Mace, S.C. Roberts, and D.W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402: 286-288.

Carr, M. M., J. Yoshizaki, F. T. van Manen, M. R. Pelton, O. C. Huygens, H. Hayashi, and M. Maekawa. 2002. A multi-scale assessment of habitat use by Asiatic black bears in central Japan. Ursus 13: 1-9.

Chhangani, A.K. 2002. Food and feeding of sloth bear (*Melursus ursinus*) in Aravalli Hills of Rajasthan, India. Tigerpaper 29: 1-6.

Chapman, C.A., L.J. Chapman, R. Wangham, K. Hunt, D. Gebo, and L. Gardner. 1992. Estimators of fruit abundance of tropical trees. Biotropica 24: 527-531.

Chinh, N.N., C.T. Chung, V.V. Can, N.X. Dung, V.V. Dung, N.K. Dao, T. Hop, T.T. Oanh, N.B. Quynh, and N.N. Thin. 1996. Vietnam forest trees. Forest Inventory and Planning Institute. Agricultural Publishing House, Hanoi, Vietnam.

Christiansen, P. 2007. Evolutionary implications of bite mechanics and feeding ecology in bears. Journal of Zoology 272: 423-443.

Clark, J. D., D. L. Clapp, K. G. Smith, and B. Ederington. 1994. Black bear habitat use in relation to food availability in the interior highlands of Arkansas. International Conference for Bear Research and Management 9: 309-318.

Clevenger, A. P., F. J. Purnoy, and M. R. Pelton. 1992. Brown bear (*Ursus arctos* L.) habitat use in the Cantabrian Mountains, Spain. Mammalia 56: 202-214.

Clevenger, A. P., F. J. Purroy, and M. A. Campos. 1997. Habitat assessment of a relict brown bear *Ursus arctos* population in northern Spain. Biological Conservation 80: 17-22.

Collins, N. M. 1980. The distribution of soil macrofauna on the west ridge of Gunung (Mount) Mulu, Sarawak. Oecologia 44: 263-275.

Collins, N. M. 1989. Termites. Pages 455-471 in: H. Leith, and M. J. A. Werger, editors. Tropical rain forest ecosystems: biogeographical and ecological studies. Elsevier Science Publishers, Amsterdam.

Colwell, J. H., and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics 6: 281-310.

Corlett, R.T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. Biological Review 73: 413-448.

Costello, C. M., and R. W. Sage. 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. International Conference for Bear Research and Management 9: 375-388.

Creel, S., G. Spong, and N. Creel. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35-60 in: J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge.

Cuesta, F., M. F. Peralvo, and F. T. van Manen. 2003. Andean bear habitat use in the Oyacachi River Basin, Ecuador. Ursus 14: 198-209.

Dang, Nguyen Xuan. 2006. The current status and conservation of bears in Vietnam. Pages 61-65 in: Understanding Asian bears to secure their future. Japan Bear Network (compiler), Ibaraki, Japan.

Davis, H., R. D. Weir, A. N. Hamilton, and J. A. Deal. 2006. Influence of phenology on site selection by female American black bears in coastal British Columbia. Ursus 17: 41-51.

Davies, T.J., S. Meiri, T.G. Barraclough, and J.L. Gittleman. 2007. Species co-existence and character divergence across carnivores. Ecology Letters 10: 146-152.

Davis, H., R.D. Weir, A.N. Hamilton, and J.A. Deal. 2006. Influence of phenology on site selection by female American black bears in coastal British Columbia. Ursus 17: 41-51.

Dayan, T. and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. Ecology Letters 8: 875-894.

Dearing, M.D. and J.J. Schall. 1992. Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophoros murinus*. Ecology 73: 845-858.

Duckworth, J. W., and S. Hedges. 1998. Tracking tigers: a review of the status of tiger, Asian elephant, gaur and banteng in Vietnam, Lao, Cambodia and Yunnan (China), with recommendations for future conservation action. World Wide Fund for Nature Indochina Programme, Hanoi, Vietnam.

Duckworth, J.W., R. E. Salter, and K. Khounboline. 1999. Wildlife in Lao PDR: 1999 status report. IUCN/WCS/Center for protected areas and watershed management, Vientiane, Lao PDR

Edenius, L. G. Ericsson, and P. Naslund. 2002. Selectivity by moose vs the spatial distribution of aspen: a natural experiment. Ecography 25: 289-294.

Erdbrink, D. P. 1953. A review of the fossil and recent bears of the old world, with remarks on their phylogeny. Deventer, The Netherlands.

Field, A. 2005. Discovering statistics using SPSS. Sage Publications, London.

Fleming, T.H., R. Breitwisch and G.H. Whitesides. 1987. Patterns of tropical vertebrate frugivore diversity. Annual Review of Ecology and Systematics 18: 91-109.

Fredriksson, G. M., S. A. Wich, and Trisno. 2006. Frugivory in sun bears (*Helarctos malayanus*) is linked to El Nino-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. Biological Journal of the Linnean Society 89: 489-508.

Fredriksson, G.M., L.S. Danielsen, and J.E. Swenson. 2007. Impacts of El Nino related drought and forest fires on sun bear fruit resources in lowland dipterocarp forest of East Borneo. Biodiversity and Conservation 16: 1823-1838.

Fryxell, J.M. and P. Lundberg. 1998. Individual behavior and community dynamics. Chapman and Hall, London.

Gardner, S., P. Sidisunthorn and V. Anusarnsunthorn. 2000. A field guide to forest trees of northern Thailand. Kobfai Publishing Project, Bangkok.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection and importance. Pages 111-153 in: L. Boitani, and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York.

Garshelis, D. L. 2004. Variation in ursid life histories–is there an outlier? Pages 53-73 in: D. Lindburg, and K. Baragona, editors. Giant pandas: Biology and conservation. University of California Press, Berkeley, California.

Garshelis, D. and R. Steinmetz. 2005. Issues and conservation priorities from the Asiatic Black Bear Expert Team. International Bear News 14: 9-12.

Gittleman, J.L. 1985. Carnivore body size: ecological and taxonomic correlates. Oecologia 67: 540-554.

Glen, A. S., and C. R. Dickman. 2008. Niche overlap between marsupial and eutherian carnivores: does competition threaten the endangered spotted-tailed quoll? Journal of Applied Ecology 45: 700-707.

Gotelli, N. J., and G. L. Entsminger. 2001. EcoSim: null models software for ecology. Acquired Intelligence and Kesey-Bear, Burlington, Vermont.

Grassman, L. I., J. E. Haines, J. E. Jenecka, and M. E. Tewes. 2006. Activity periods of photo-captured mammals in north-central Thailand. Mammalia 70: 306-309.

Grenwood, J.J.D. and R.A. Elton. 1979. Analysing experiments on frequency-dependent selection by predators. Journal of Animal Ecology 48: 721-737.

Guthery, F. S., and R. L. Bingham. 2007. A primer on interpreting regression models. Journal of Wildlife Management 71: 684-692.

Hanski, I. 1995. Effects of landscape pattern on competitive interactions. Pages 203-220 in: L. Hansson, L. Fahrig, and H. G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London.

Hara, M., M. Kanzaki, T. Mzuno, H. Noguchi, K. Sri-Ngernyuang, S. Teejuntuk, C. Sungpalee, T. Ohkubo, T. Yamakura, P. Sahunalu, P. Dhanmanonda, and S. Bunyavejchewin. 2002. The floristic composition of tropical montane forest in Doi Inthanon National Park, northern Thailand, with special reference to its phytogeographical relation with montane forests in tropical Asia. Natural History Research 1: 1-17.

Herrera, C.M. 2002. Seed dispersal by vertebrates. Pp. 185-208 in: Herrera, C.M. and O. Pellour, editors. Plant-animal interactions: an evolutionary approach. Blackwell Publishing, Malden, Massachusetts.

Herrero, S. 1978. A comparison of some features of the evolution, ecology, and behavior of black and grizzly/brown bears. Carnivore 1: 7-17.

Holm, G. W., F. G. Lindzey, and D. S. Moody. 1999. Interactions of sympatric black and grizzly bears in northwest Wyoming. Ursus 11:99-108.

Holt, R. D. 2001. Species coexistence. Encyclopedia of Biodiversity 5: 413-426.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149: 745-764.

Htun, S. 2006. The status and conservation of bears in Myanmar. Pages 45-49 in: Understanding Asian bears to secure their future. Japan Bear Network (compilers), Ibaraki, Japan.

Huygens, O.C. and H. Hayashi. 2001. Use of stone pine seeds and acorns by Asiatic black bears in central Japan. Ursus 12: 47-50.

Huygens, O. C., T. Miyashita, B. Dahle, M. Carr, I. Izumiyama, T. Sugawara, and H. Hayashi. 2003. Diet and feeding of Asiatic black bears in the Northern Japanese Alps. Ursus 14: 236-245.

Hwang, M.-S., D. L. Garshelis, and Y. Wang. 2002. Diets of Asiatic black bears in Taiwan, with methodological and geographical comparisons. Ursus 13: 111-125.

Izumiyama, S. and T. Shiraishi. 2004. Seasonal changes in elevation and habitat use of the Asiatic black bear (*Ursus thibetanus*) in the Northern Japan Alps. Mammal Study 29: 1-

8.

Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. T. Robbins, and R. T. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63: 921-929.

James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's box? Annual Review of Ecology and Systematics 21: 129-166.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19: 101-108.

Jordano, P. 1992. Fruits and frugivory. Pp 105-156 in: M. Fenner, editor. Seeds, the ecology of regeneration on plant communities. CAB International, Oxon, UK

Joshi, A.R., D.L. Garshelis and J.L.D. Smith. 1997. Seasonal and habitat-related diets of sloth bears in Nepal. Journal of Mammalogy 78: 584-597.

Kanzaki, M. K. Yoda, and P. Dhanmanonda. 1995. Mosaic structure and tree growth pattern in a monodominant tropical seasonal evergreen forest in Thailand. Pages 25-41 in: E.O. Box, R.K. Peet, T. Masuzawa, I. Yamada, and K. Fugiwara, editors. Vegetation science in forestry. Kluwer Academic Publishers, Dordrecht, Netherlands.

Karamanlidis, A.A., Y. Dionisios, S. Sgardelis, and Z. Scouras. Using sign at power poles to document presence of bears in Greece. Ursus 18: 54-61.

Karanth, K.U. and M.E. Sunquist. 1995. Prey selection by tiger, leopard and dhole tropical forests. Journal of Animal Ecology. 64: 439-450.

Kitamura, S. 2000. Seed dispersal by hornbills in a tropical rain forest in Khao Yai national park, Thailand. MSc. Thesis, Kyoto University, Kyoto.

Kitamura, S., T. Yumoto, P. Poonswad, P. Chuailua, K. Plongmai, T. Maruhashi, N. Noma. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. Oecologia 133: 559-572.

Kitamura, S., S. Suzuki, T. Yumoto, P. Chuailua, K. Plongmai, P. Poonswad, N. Noma, T. Maruhashi, C. Suckasam. 2005. A botanical inventory of a tropical seasonal forest in Khao Yai National Park, Thailand: implications for fruit-frugivore interactions. Biodiversity and Conservation 14: 1241-1262.

Kitchener, A.M., E.M. Gese, and E.R. Schauster. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77: 164-1656.

Krause, J., T. Unger, A. Nocon, A. Malaspinas, S. Kolokotronis, M. Stiller, L. Soibelzon, H. Spriggs, P.H. Dear, A.W. Briggs, S. Bray, S. O'Brien, G. Rabeder, P. Matheus, A. Cooper, M. Slatkin, S. Paabo, and M. Hofreiter. 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears nears the Miocene-Pliocene boundary. BMC Ecology 8: 220-231.

Krebs, C.J. 1999. Ecological methodology (2nd ed.). Addison Wesley Longman, Inc., Menlo Park, California.

Kotler, B. J., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19: 281-308.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology and Systematics 34: 153-181.

La Combe, C. 2008. Big news about bears in Bangladesh. Dhaka Courier 24: 16-18.

Laing, S.E., S.T. Buckland, R.W. Burns, D. Lambie, and A. Amphlett. 2003. Dung and nest surveys: estimating decay rates. Journal of Applied Ecology 40: 1102-1111.

Landau, S. and B. S. Everitt. 2004. A handbook of statistical analyses using SPSS. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Landers, J. L., R. J. Hamilton, A. S. Johnson, and R. L. Marchinton. 1979. Foods and habitat of black bears in North Carolina. Journal of Wildlife Management 43: 143-153.

Leighton, M. & D.R. Leighton. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp. 181-196 in: Sutton, S.L., T.C. Whitmore, & A.C. Chadwich, editors. Tropical rainforest: ecology and management. Blackwell Science Publishing,

London.

Leighton, M. 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. International Journal of Primatology 14: 257-313.

Lekagul, B., and J. A. McNeely 1988. Mammals of Thailand. Association for the Conservation of Wildlife, Bangkok.

Leon, J.A. and D.B. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. Journal of Theoretical Biology 50: 185-193.

Lewison, R., E. L. Fitzhugh, and S. P. Galentine. 2001.Validation of a rigorous track classification technique: identifying individual mountain lions. Biological Conservation 99: 313–321.

Lindzey, F. G., and E. C. Meslow. 1977. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41: 413-425.

Linkie, M., Y. Dinata, A. Nugroho, and I. A. Haidir. 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. Biological Conservation 137:20-27.

Lynam, A.J. 2003. A national tiger action plan for the Union of Myanmar. Myanmar Forest Department and Wildlife Conservation Society, International Program.

Lynam, A.J., P.D. Round, and W.Y. Brockelman. 2006. Status of birds and large mammals in Thailand's Dong Phayayen-Khao Yai forest complex. Biodiversity Research and Training Program (BRT) and Wildlife Conservation Society, Bangkok.

Manjrekar, N. 1989. Feeding ecology of the Himalayan black bear (*Selenarctos thibetanus* Cuvier) in Dachigam National Park. Masters Thesis. Saurashtra University, Rajkot, India.

Martin, T.E. and G.R. Guepel. 1993. Nest monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507-519.

Mattson, D. J., C. M. Gillin, S. A. Benson, and R. R. Knight. 1991. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. Canadian Journal of Zoology 69: 2430-2435.

Mattson, D. J., S. Herrero, and T. Merrill. 2005. Are black bears a factor in the restoration of North American grizzly bear populations? Ursus 16: 11-30.

Mattson, D. J. 2003. Foot loadings and pad and track widths of Yellowstone grizzly bears. Western North American Naturalist 63: 72–79.

Maxwell, J. F. 1995. Vegetation and vascular flora of the Ban Saneh Pawng area, Lai Wo Subdistrict, Sangklaburi District, Kanchanaburi Province, Thailand. Natural History Bulletin of the Siam Society 43: 131-170.

Mazza, P. and M. Rustioni. 1994. On the phylogeny of Eurasian bears. Paleontographica 230: 1-38.

McConkey, K. and M. Galetti. 1999. Seed dispersal by the sun bear *Helarctos malayanus* in Central Borneo. Journal of Tropical Ecology 15: 237-241.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21: 178-185.

McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia 132: 102-108.

Meijaard, E. 2004. Craniometric differences among Malayan sun bears (*Ursus malayanus*); evolutionary and taxonomic implications. The Raffles Bulletin of Zoology 52: 665–672.

Nakasathien, S., and B. Stewart-Cox. 1990. Nomination of Thung Yai-Huai Kha Khaeng Wildlife Sanctuary to be a UNESCO World Heritage Site. Royal Forest Department, Bangkok.

Nea, C. and D. Nong. 2006. The conservation of bears in Cambodia. Pages 57-60 in: Understanding Asian bears to secure their future. Japan Bear Network (compiler), Ibaraki, Japan.

Neale, J. C. C., and B. N. Sacks. 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. Oikos 94: 236-249.

Ng'andu, N.H. 1997. An empirical comparison of statistical tests for assessing the proportional hazards assumption of Cox's model. Statistics in Medicine 16: 611-626.

Noyce, K.V. and P.L. Coy. 1990. Abundance and productivity of bear food species in different forest types of northcentral Minnesota. Ursus 8: 169-181.

Nozaki, E., S. Azuma, T. Aoi, H. Torii, T. Ito and K. Maeda. 1983. Food habits of Japanese black bear. International Conference on Bear Research and Management 5: 106-109.

Owen-Smith, N. and P. Novellie. 1982. What should a clever ungulate eat? American Naturalist 119: 151-178.

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61: 102-112.

Perry, G. and E.R. Pianka. 1997. Animal foraging: past, present and future. Trends in Ecology and Evolution 12: 360-364.

Phoonjampa, R. 2002. Using ants as indicators of plant communities at Khao Yai National Park, Thailand. Masters Thesis. Kasetsart University, Bangkok.

Plumptre, A.J. and V. Reynolds. 1996. Censusing Chimpanzees in the Ubongo forest, Uganda. International Journal of Primatology 17: 85-99.

Pollock, K.H., S.R. Winterstein, C.M. Bunck, and P.D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of wildlife management 53: 7-15.

Poscillico, M., A. Meriggi, E. Pagnin, S. Lovari, and L. Russo. 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. Biological Conservation 118: 141-150.

Primack, R. and R. Corlett. 2005. Tropical rain forests: an ecological and biogeographical comparison. Blackwell Publishing, Malden.

Prugh, L.R. and C.J. Krebs. 2004. Snowshoe hare pellet-decay rates and aging in different habitats. Wildlife Society Bulletin 32: 386-393.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, United Kingdom.

Reid, D., Q. Jiang, Z. Teng, Z. Qin, and J. Hu. 1991. Ecology of the Asiatic black bear (*Ursus thibetanus*) in Sichuan, China. Mammalia 55: 221-237.

Riggs, M.R. and K.H. Pollock. 1992. A risk ratio approach to multivariate analysis of survival in longitudinal studies of wildlife populations. Pages 74-89 in D.R. McCullough and R.H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, London.

Rios-Uzeda, B., H. Gomez, and R. B. Wallace. 2006. Habitat preferences of the Andean bear (*Tremarctos ornatus*) in the Bolivian Andes. Journal of Zoology 268: 271-278.

Ritchie, M. 2002. Competition and coexistence in mobile animals. Pages 109-131 in: U. Sommer, and B. Worm, editors. Competition and coexistence. Springer-Verlag, Berlin.

Robbins, C.T. 1993. Wildlife feeding and nutrition. Academic Press, New York.

Rode, K.D. and C.T. Robbins. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78: 1640-1645.

Rosenzweig, M.L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47: 602-612.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. American Naturalist 137 (Supplement): S5-S28.

Rotenberry, J.T. 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment? Ecological Monographs 50: 93-110.

Rundel, P.W. and K. Boonpragob. 1995. Dry forest ecosystems of Thailand. Pp. 93-119 in: Bullock, S.H., H.A. Mooney, and E. Medina (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Saberwal, V. 1989. Distribution and movement patterns of the Himalayan black bear (*Selenarctos thibetanus* Cuvier) in Dachigam National Park, Kashmir. MSc. Thesis. Saurashtra University, Rajkot, India.

Sacco, T. and B. Van Valkenburgh. 2004. Ecomorphological indicators of feeding behavior in the bears (Carnivora: Ursidae). Journal of Zoology 263: 41-54.

Sahunalu, P. and P. Dhanmanonda. 1995. Structure and dynamics of dry dipterocarp forest, Sakaerat, northeastern Thailand. Pages 465-494 in: R. Tuxes and H. Lieth, editors. Handbook of vegetation science. Kluwer Academic Publishers, Dordrecht, Netherlands.

Sale, P.F. 1974. Overlap in resource use, and interspecific competition. Oecologia 17: 245-256.

Sanchez, D.M., P.R. Krausman, T.R. Livingston, and P.S. Gipson. 2004. Persistence of carnivore scat in the Sonoran Desert. Wildlife Society Bulletin 32: 366-372.

Sanderson, E., J. Forrest, C. Loucks, J. Ginsberg, E. Dinerstein, J. Seidensticker, P. Leimgruber, M. Songer, A. Heydlauff, T. O'Brien, G. Bryja, S. Klenzendorf, and E. Wikramanayake. 2006. Setting priorities for the conservation and recovery of wild tigers: 2005-2015, The Technical Assessment. WCS, WWF, Smithsonian, and NFWF-STF, New York and Washington D.C.

Sathyakumar, S. and S. Viswanath. 2003. Observations on food habits of Asiatic black bear in Kedarnath Wildlife Sanctuary, India: preliminary evidence on their role in seed germination and dispersal. Ursus 14: 99-103.

Schaller, G. B., Q. T. Teng, K. G. Johnson, X. M. Wang, H. M. Shen, and J. C. Hu. 1989. The feeding ecology of giant pandas and Asiatic black bears in the Tangjiahe Reserve, China. Pages 212-241 in: J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, New York.

Schoen, J. W. 1990. Bear habitat management: a review a future perspective. International Conference for Bear Research and Management 8: 143-154.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Schoener, T.W. 1983. Field experiments on interspecific competition. American Naturalist 122: 240-285.

Schoener, T. W. 1986. Resource partitioning. Pages 91-126 in: J. Kikkawa, and D. J. Anderson, editors. Community ecology: pattern and process. Blackwell Scientific Publications, Melbourne.

Servheen, C., S. Herrero, and B. C. Peyton 1999. Bears - status survey and conservation action plan. IUCN/SSC Bear and Polar Bear Specialist Groups, Gland, Switzerland.

Servheen, C. 2001. The status of the bears of the world with emphasis on Asia. Pages 4-9 in: D. Williamson and M.J. Phipps, editors. Proceedings of the 3rd international symposium on the trade in bear parts, 26-28 October 1999, Seoul, Republic of Korea. TRAFFIC East Asia, Hong Kong.

Sharma, S., Y. Jhala, and V. B. Sawarkar. 2003. Gender discrimination of tigers by using their pugmarks. Wildlife Society Bulletin 31: 258–264.

Sharma, S., Y. Jhala, and V. B. Sawarkar. 2005. Identification of individual tigers (*Panthera tigris*) from their pugmarks. Journal of Zoology (London) 267: 9–18.

Skarpe, C., R. Bergstrom, A.L. Bratan, and K. Danell. 2000. Browsing in a heterogeneous savanna. Ecography 23: 632-640.

Smallwood, K. S., and E. L. Fitzhugh. 1993. A rigorous technique for identifying individual mountain lions *Felis concolor* by their tracks. Biological Conservation 65: 51–59.

Smith, R.L. and T.M. Smith. 2001. Ecology and field biology. Benjamin Cummings, San Francisco.

Snow, D.W. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica 13: 1-14.

Sreekumar, P.G. and M. Balakrishnan. 2001. Seed dispersal by the Sloth bear (*Melursus ursinus*) in South India. Biotropica 34: 474-477.

Steinmetz, R., T. Stones, and T. Chan-aed. 1999. An ecological survey of habitats, wildlife, and people in Xe Sap National Biodiversity Conservation Area, Saravan Province, Lao PDR. World Wide Fund for Nature-Thailand Program, Bangkok, Thailand.

Steinmetz, R. 2004. Gaur (*Bos gaurus*) and banteng (*B. javanicus*) in the lowland forest mosaic of Xe Pian protected area, Lao PDR: abundance, habitat use, and conservation. Mammalia 68: 141–157.

Steinmetz, R., W. Chutipong, and N. Seuaturien. 2006. Collaborating to conserve large mammals in Southeast Asia. Conservation Biology 20: 1391-1401.

Steinmetz, R., N. Seuaturien, W. Chutipong, C. Chamnankit, and R. Phoonjampa. 2007. The ecology and conservation of tigers, other large carnivores, and their prey in Kuiburi National Park, Thailand. WWF-Thailand and Department of National Parks, Wildlife, and Plant Conservation, Bangkok, Thailand.

Steinmetz, R., M. Hunt, G. Fredriksson, and A. Olsson. 2007. Bear sign-survey training held in Cambodia. International Bear News 16: 6-9.

Steinmetz, R. W. Chutipong, N. Seuaturien, and E. Chirngsaard. 2008. Community structure of large mammals in tropical montane and lowland forests in the Tenasserim-Dawna Mountains, Thailand. Biotropica 40: 344-353.

Steinmetz, R., and D. L. Garshelis. 2008. Distinguishing Asiatic black bears and sun bears by claw marks on climbed trees. Journal of Wildlife Management 72: 814-821.

Stirling, I., and A. E. Derocher. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. International Conference on Bear Research and Management 8: 189–204.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. J. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83: 229-244.

Stibig, H.-J., and R. Beuchle. 2003. Forest cover map of continental Southeast Asia at 1:4,000,000. TREES Publications Series D: Thematic outputs no. 4. Institute for Environment and Sustainability, Germany.

Stiles, E.W. 1993. The influence of pulp lipids on fruit preference by birds. Pages 227-235 in: T.H. Fleming and A. Estrada, editors. Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic Publishers, Dordrecht, Netherlands.

Stone, L. and A. Roberts. 1990. The checkerboard score and species distributions. Oecologia 85: 74-79.

Takahashi, K., T. Shiota, H. Tamatani, M. Koyama, and I. Washitani. 2007. Seasonal variation in fleshy fruit use and seed dispersal by the Japanese black bear (*Ursus thibetanus japonicus*). Ecological Research 23: 471-478.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pages 330-344 in: M.E. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland.

Theberge, J. B., and C. H. Wedells. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67: 1285-1290.

Tougard, C. 2001. Biogeography and migration routes of large mammal faunas in South-east Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand. Paleogeograhy, Paleoclimatology, Paleoecology 168: 337-358.

Tumbelaka, L., and G. M. Fredriksson. 2006. The status of sun bears in Indonesia. Pages 73-78 in: Understanding Asian bears to secure their future. Japan Bear Network (compiler), Ibaraki, Japan.

Turner, I.M. 2001. The ecology of trees in the tropical rain forest. Cambridge University Press, Cambridge, United Kingdom.

van de Bult, M. 2003. The vegetation and flora of the Western Forest Complex. Department of National Parks, Wildlife, and Plant Conservation, Bangkok.

van Schaik, C.P., J.W. Terborgh, and S.J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24: 353-377.

Van Steenis, C.G.G.J. 1978. Flora Malesiana. Series 1, volume 8. P. Noordhoff, Leyden.

Vinitpornsawan, S., R. Steinmetz, and B. Kanchanasakha. 2006. The status of bears in Thailand. Pages 50-56 in: Japan Bear Network (compiler). Understanding Asian bears to secure their future. Japan Bear Network, Ibaraki, Japan.

Wang, D., S. Li, W.J. McShea, and M.F. Li. 2006. Use of remote-trip cameras for wildlife surveys and evaluating the effectiveness of conservation activities at a nature reserve in Sichuan Province, China. Environmental Management 38: 942–951.

Webb, E. L. 2007. Botanical exploration of Thung Yai Naresuan Wildlife Sanctuary, western Thailand. Asian Institute of Technology, Patumthani, Thailand.

Wei, F., Z. Feng, Z. Wang, and J. Hu. 2000. Habitat use and separation between the giant panda and the red panda. Journal of Mammalogy 81:448-455.

Welch, C.A., J. Keay, K.C. Kendall and C.T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78: 1105-1119.

Westoby, M. 1978. What are the biological bases of varied diets? American Naturalist 112: 627-631.

Wheelwright, N.T., W.A. Haber, K.G. Murray and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of Costa Rican lowland moist forest. Biotropica 16: 173-192.

Wiens, J.A. 1993. Fat times, lean times, and competition among predators. Trends in Ecology and Evolution 8: 348-349.

Wemmer, C., T.H. Kunz, G. Lundie-Jenkins, and W.J. McShea. 1996. Mammalian sign. Pages 157-176 in: D.E. Wilson, F.R. Cole, J.D. Nichols, R. Rudran, and M.S. Foster, editors. Measuring and monitoring biological diversity, standard methods for mammals. Smithsonian Institution Press, Washington, D.C.

Wisheu, I. C. 1998. How organisms partition habitats: different types of community organization can produce identical patterns. Oikos 83: 246-258.

Wong, S. T., C. W. Servheen, and L. Ambu. 2002. Food habits of Malayan sun bears in lowland tropical forests of Borneo. Ursus 13: 127-136.

Wong, S. T., C. Servheen, and L. Ambu. 2004. Home range, movement and activity patterns, and bedding sites of Malayan sun bears *Helarctos malayanus* in the rainforest of Borneo. Biological Conservation 119: 169-181.

Wong, S.T., C.W. Servheen, L. Ambu, and A. Norhayati. 2005. Impacts of fruit production cycles on Malaysian sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. Journal of Tropical Ecology 21: 627-639.

Wong, S.T. 2006. The status of Malayan sun bear in Malaysia. Pages 66-72 in: Understanding Asian bears to secure their future. Japan Bear Network (compiler), Ibaraki, Japan.

Wooding, J. B., and T. S. Hardisky. 1994. Home range, habitat use, and mortality of black bears in north-central Florida. International Conference for Bear Research and Management 9: 349-356.

Yasuda, M., S. Miura, N. Ishii, T. Okuda, and N.A. Hussein. 2005. Fallen fruits and terrestrial vertebrate frugivores: a case study in a lowland tropical rainforest in peninsular Malaysia. Pages 151-173 in: P.M. Forget, J.E. Lambert, P.E. Hulme, and S.B. Venderwall, editors. Seed fate: predation, dispersal, and seedling establishment. CABI, Massachusetts, USA.

Zalewski, A. 1999. Identifying sex and individuals of pine marten using snow track measurements. Wildlife Society Bulletin 27: 28–31.

Zielinski, W. J., and R. L. Truex. 1995. Distinguishing tracks of marten and fisher at track-plate stations. Journal of Wildlife Management 59: 571–579.

Appendix 1. Plant taxa used (i.e., climbed or eaten) by sun bears and black bears, as determined from bear signs in 3 forest types in Thung Yai Naresuan Wildlife Sanctuary, 2001–2003. SEF = semi-evergreen forest; MDF = mixed deciduous forest; MEF = montane evergreen forest. Values in parentheses are percent of all climbed trees in a forest type from that family (values do not apply to genera or species, nor to non-tree families). No value indicates that no trees from that family were used in that forest type. [1]Not a tree family. x* = seeds in scat identified only to genus or family.

			Forest type in which taxa used (x)			Bear signs				
						Climbed trees				Other
Family	Genera	Species	SEF	MDF	MEF	Broken branch	Multiple climbing events	Fresh marks on fruiting tree	Claw marks only	Scat, Feeding debris
Aceraceae	*Acer*	*oblongum*	x (0.3)	(4.5)					x	
Alangiaceae	*Alangium*	*kurzii*	x (0.5)						x	
Anacardiaceae	*Lannea*	*coromandelica*	(2.4)	x					x	
	Mangifera	*caloneura*	x					x		
	Rhus	*chinensis*		x						x
	Semecarpus	*cochinchinensis*	x	x				x	x	
	Spondias	*pinnata*	x	x				x		
Annonaceae	*Cyathocalyx*	cf. *martabanicus*	x (4.2)						x	
	Polyalthia	*simiarum*	x					x	x	
	Polyalthia	*viridis*	x						x	
	Polyalthia	sp.	x						x	
	Pseuduvaria	sp.	x						x	
	unidentified	sp.1	x						x	
	unidentified	sp.2	x						x	
Apocynaceae	*Alstonia*	*rostrata*	x (1.0)			x				
Araceae[1]	*Alocasia*	sp.								x
Araliaceae	*Schefflera*	*pueckleri*	x (0.5)			x				
Aquifoliaceae	*Ilex*	sp.			x (1.5)				x	
Bignoniaceae	*Fernandoa*	*adenophylla*		x (7.6)		x	x			
	Markhamia	*stipulata*	x (0.3)						x	
	Stereospermum	*colais*		x		x				
	Stereospermum	*neuranthum*		x		x				
Bombacaceae	*Bombax*	*anceps*		x (0.6)					x	
Burseraceae	*Canarium*	*subulatum*	x (0.8)	x (3.8)				x		
	Garuga	*pinnata*	x	x					x	
Caprifoliaceae	*Viburnum*	*punctatum*	x (0.3)						x	
Celestraceae	*Euonymus*	*cochinchinensis*	x (4.7)	(0.6)				x	x	
	Euonymus	*colonoides*	x					x	x	
	Lophopetalum	*wallichii*	x	x		x				
Combretaceae	*Terminalia*	*alata*	(0.8)	x (5.1)					x	
	Terminalia	*bellirica*	x	x				x		
	Terminalia	*chebula*		x				x		

Family	Genus	Species						
	Terminalia	*mucronata*		x			x	x	
Cornaceae	*Mastixia*	cf. *euonymoides*	x (0.3)					x	
Datiscaceae	*Tetrameles*	*nudiflora*	x (0.5)					x	
Dilleniaceae	*Dillenia*	*ovata*		x (8.9)			x	x	
	Dillenia	*parviflora*	x (0.5)				x	x	
Dipterocarpaceae	*Shorea*	*obtusa*		x (3.8)				x	
	Shorea	*siamensis*		x				x	
Ebenaceae	*Diospyros*	*ehretioides* or *glandulosa*		x					x
Eleocarpaceae	*Eleocarpus*	cf. *griffithii*	(2.1)	(0.6)	x (1.5)			x	
	Eleocarpus	*prunifolius*	x				x		
	Eleocarpus	cf. *rugosa*	x					x	
	Eleocarpus	*stipularis*	x					x	
	Eleocarpus	sp.1	x					x	
	Eleocarpus	sp.2	x					x	
	Eleocarpus	sp.3	x					x	
	Eleocarpus	sp.4		x			x		
Euphorbiaceae	*Antidesma*	*bunius*	x (3.7)	(2.5)			x		x
	Aporosa	*dioica*		x				x	
	Baccaurea	*ramiflora*	x				x	x	x
	Balakata	*baccata*	x					x	
	Bischofia	*javanica*	x					x	
	Bridelia	*anceps*		x				x	
	Bridelia	*glauca*		x				x	
	Bridelia	sp.	x					x	
	Macaranga	*denticulata*		x				x	
	Mallotus	*paniculatus*	x					x	
	Mallotus	sp.	x					x	
	Trewia	*nudiflora*	x					x	
	unidentified	sp.	x					x	
Fagaceae	*Castanopsis*	*tribuloides*	(7.9)	x (6.4)	(29.2)		x	x	
	Castanopsis	sp.1	x					x	
	Castanopsis	sp.2	x					x	
	Lithocarpus	*aggregatus*			x	x	x		
	Lithocarpus	*elegans*	x				x	x	
	Lithocarpus	*fenestratus*	x		x		x		
	Lithocarpus	*polystachyus*	x					x	
	Lithocarpus	*truncatus*	x		x		x	x	
	Quercus	*brandisiana*		x		x		x	
	Quercus	*kerrii*		x		x		x	
	Quercus	*semiserrata*	x		x	x	x	x	x
Flacourtiaceae	*Casearia*	*grewiifolia*	x (1.0)				x		
	Casearia	*mekongii*							x
Guttiferae	*Calophyllum*	sp.			x (3.1)			x	
	Garcinia	sp.	x				x		
Hammamelidaceae	*Altingia*	*excelsa*	x (0.3)					x	
Icacinaceae	*Apodytes*	*dimidiata*	x (4.7)		(1.5)				x
	Gomphandra	*tetrandra*			x	x			

Family	Genus	Species							
	Gomphandra	*quadrifida*	x				x		
	Platea	*latifolia*	x				x		
Juglandaceae	*Engelhardia*	*spicata*	x (0.3)				x	x	
Labiatae	*Callicarpa*	*arborea*	(0.8)	x (11.5)					x
	Gmelina	*arborea*		x				x	
	Premna	*latifolia*		x					x
	Premna	*villosa*		x					x
	Vitex	*peduncularis*		x		x	x		
	Vitex	*quinata*	x	x					x
Lauraceae	*Alseodaphne*	*nigrescens*	x (21.5)	(3.2)	(32.3)		x		
	Beilschmiedia	sp.	x				x		
	Cinnamomum	*caudatum*	x	x			x		
	Cinnamomum	*iners*	x		x		x		
	Cinnamomum	*porrectum*	x				x	x	
	Cinnamomum	sp. 1			x				x
	Cinnamomum	sp. 2	x						x
	Cryptocarya	sp.	x		x				x
	Dehaasia	*cuneata*	x						x
	Litsea	*cf. salicifolia*	x	x		x			
	Litsea	*garrettii*	x				x		
	Litsea	sp.	x						x
	Nothaphoebe	*umbelliflora*	x				x		
	Phoebe	*cathia*	x		x		x		
	Phoebe	*lanceolata*	x	x	x		x		
	Phoebe	*cf. paniculata*			x		x		
	Phoebe	sp.	x				x		
	unidentified	sp.1	x						x
	unidentified	sp.2	x				x		
	unidentified	sp.3			x		x		
Lecythidaceae	*Barringtonia*	*acutangula*	x (0.8)				x		
Leguminosae	*Albizia*	*chinensis*	(1.3)	x (12.2)					x
	Callerya	*atropurpurea*	x				x		
	Cassia	*fistula*		x			x		x
	Dalbergia	*cf. cana*		x					x
	Dalbergia	sp.		x			x		x
	Erythrina	*subumbrans*	x				x		
	Erythrina	sp.	x				x		
	Millettia	*brandisiana*		x					x
	Pterocarpus	*macrocarpus*		x					x
	unidentified	sp.	x						x
Lythraceae	*Lagerstroemia*	*tomentosa*	x (0.8)	x (1.9)			x	x	
Magnoliaceae	*Michelia*	*baillonii*	x (5.0)	x (1.3)	(1.5)		x	x	
	Michelia	*champaca*	x						x
	Magnolia	*liliifera*	x						x
	Magnolia	*henryi*	x		x		x	x	
Meliaceae	*Aglaia*	*spectabilus*	x (8.1)	(0.6)			x	x	x*
	Chisocheton	sp.	x						x
	Chukrasia	*cf. tabularis*	x				x		

Family	Genus	Species								
	Dysoxylum	*excelsum*	x				x			
	Dysoxylum	sp.		x					x	
	Sandoricum	*koetjape*	x				x	x		
	unidentified	sp.	x						x	
Moraceae	*Artocarpus*	*lakoocha*	(2.6)	x (1.9)					x	
	Artocarpus	sp.	x						x	
	Ficus	*benjamina*	x				x	x		x*
	Ficus	*virens*	x				x			
	Ficus	*variegata*	x				x	x		
	Ficus	*cf. lacor*		x			x	x		
	Ficus	sp.1	x				x			
	Ficus	sp.2		x					x	
Musaceae[1]	*Musa*	sp.								x
Myristicaceae	*Horsefieldia*	*glabra*	x (3.4)				x			
	Horsefieldia	sp.	x				x			
	Knema	sp.	x				x			
Myrtaceae	*Syzygium*	*albiflora*	x (1.6)	(4.5)	(9.2)				x	
	Syzygium	*cumini*		x			x	x		
	Syzygium	*megacarpa*	x						x	
	Syzygium	sp.1			x				x	
	Syzygium	sp.2			x				x	
	Syzygium	sp.3	x	x		x	x	x		
	Syzygium	sp.4	x						x	
	Syzygium	sp.5	x				x			
Oleaceae	*Chionanthes*	*ramiflorus*	x (2.1)	x (0.6)				x		
Palmae[1]	(rattan)	sp.								x
Pandanaceae[1]	*Pandanus*	sp.								x
Polyosmaceae	*Polyosma*	*elongata*			x (1.5)				x	
Rhamnaceae	*Ziziphus*	*rugosa*		x (0.6)				x		x
Rosaceae	*Eriobotrya*	*bengalensis*	x (1.8)	(0.6)			x			
	Prunus	*cerasoides*	x	x					x	
Rubiaceae	*Canthium*	sp.	x (0.3)	(0.6)			x			
	Indlandia	*tinctoria*		x					x	
Sapotaceae	unidentified	sp.								x*
Sabiaceae	*Meliosma*	*simplicifolia*	x (0.3)						x	
Sapindaceae	*Dimocarpus*	*longan*	x (5.2)	x (7.6)		x		x		
	Lepisanthes	sp.	x						x	
	Litchi	*chinensis*		x		x	x	x		
	Nephelium	*hypoleucum*	x				x	x		
	Schleichera	*oleosa*		x		x	x	x		
	Mischocarpus	*pentopetalus*	x						x	
Sonneratiaceae	*Duabanga*	*grandiflora*	x (1.0)	x (0.6)					x	
Sterculiaceae	*Firmiana*	*colorata*	x (2.4)						x	
	Pterospermum	*cinnamonemum*	x						x	
	Pterocymbium	*macranthum*	x						x	
	Sterculia	*pexa*		x					x	
	Sterculia	*urena*	x	x			x			
	Sterculia	sp.	x						x	
Symplocaceae	*Symplocos*	*macrophylla*	x (1.0)				x			

Family	Genus	species						
	Symplocos	*sumnita*	x			x		x
	Symplocos	sp.	x				x	
Theaceae	*Camellia*	*connata*	(0.8)	(0.6)	x (18.5)		x	
	Pyrenaria	*garrettiana*	x		x		x	
	Ternstroemia	*gymnanthera*		x	x	x	x	
	unidentified	sp.			x		x	
Tiliaceae	*Berrya*	*cf. cordifolia*	x (1.6)	(7.0)			x	
	Berrya	*mollis*		x			x	
	Colona	*cf. winitii*		x		x	x	
	Grewia	*eriocarpa*		x		x	x	
Ulmaceae	*Gironniera*	*nervosa*	x (0.3)		x (1.5)		x	
Unidentified			(6.5)	(3.8)	(1.5)		x	
Total climbed trees			412	168	68			

Appendix 2. Map of bear distribution, and photographs

Distribution of sun bears and Asiatic black bears in Southeast Asia

Legend:

- **Evergreen Mountain Forest (>1000 m)**
- **Evergreen Lowland Forest (<1000 m)**
- **Degraded Evergreen Forest**
- **Deciduous Forest**
- **Evergreen Shrubland, Regrowth Mosaics**
- **Deciduous Shrubland, Regrowth Mosaics**
- **Mosaics of Cropping and Regrowth**
- Other Land
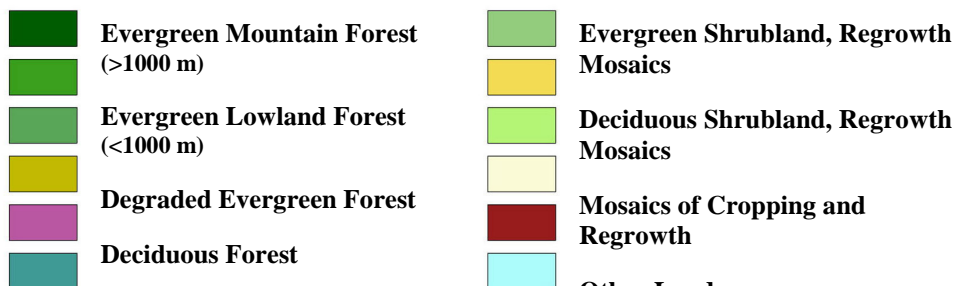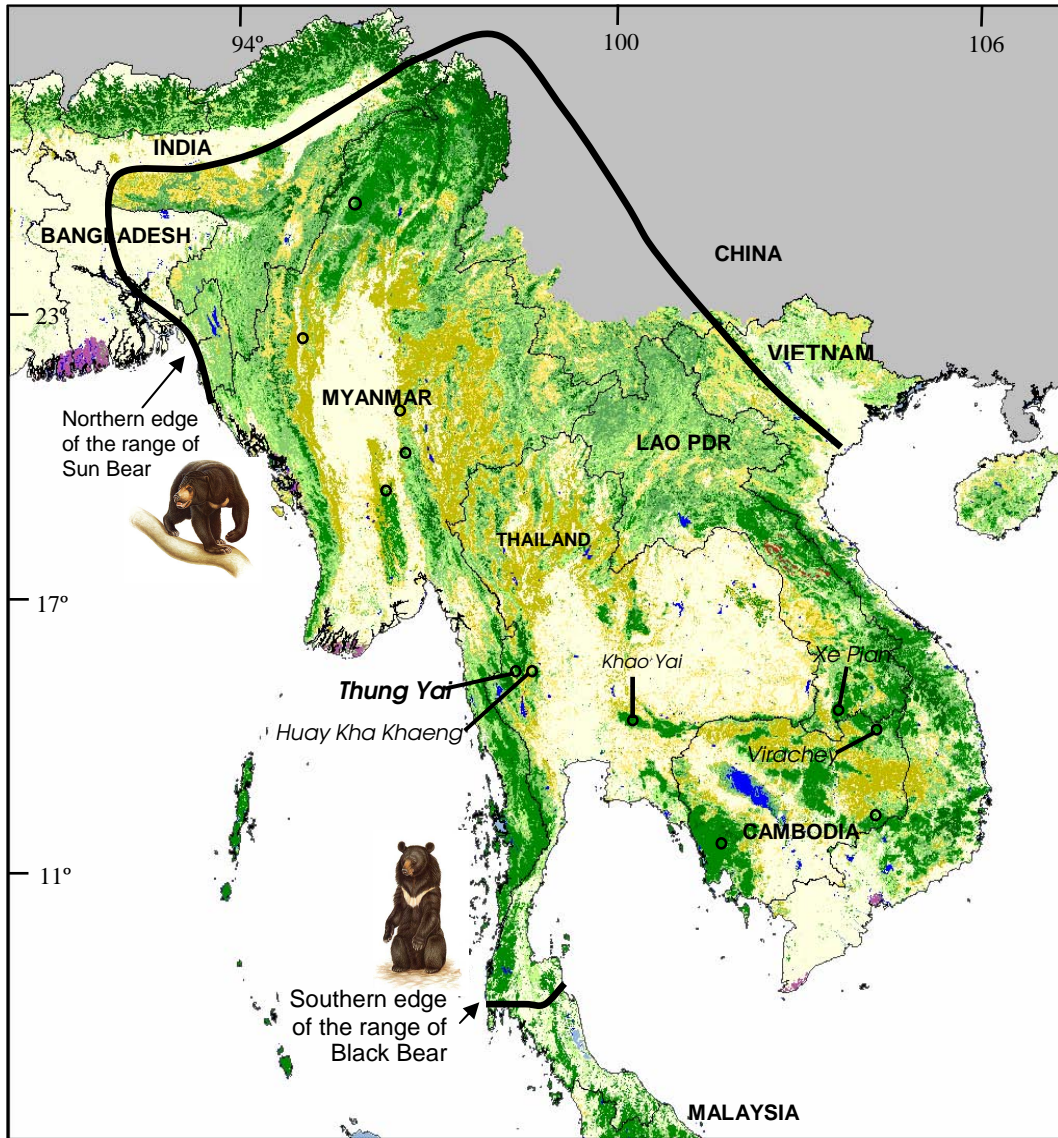
Sun bears, Asiatic black bears, and their habitats in Thung Yai

Sun bear	Asiatic black bear
Sun bear in Thung Yai	Black bear in Thailand
Semi-evergreen forest	Mixed deciduous forest

Montane evergreen forest

Field signs of bears

Claw marks

Opened rotten log

Digging for insects

Nest

Opened bee nest (*Trigona* sp. stingless bees)
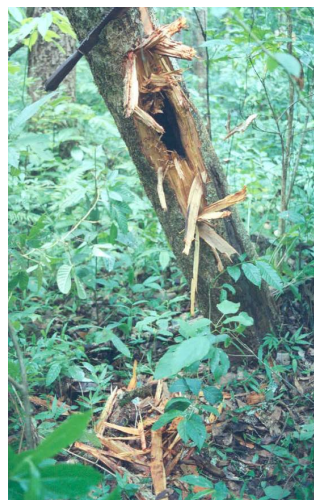
Broken branch
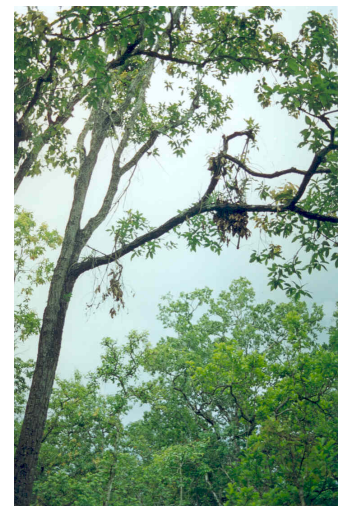
Scat

Bear fruits in Mixed Deciduous Forest

Schleichera oleosa
Sapindaceae

Cassia fistula
Leguminosae

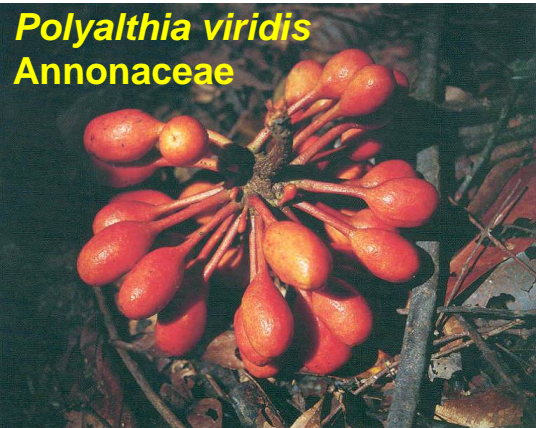### *Syzygium cumini* Myrtaceae

Quercus kerrii Fagaceae

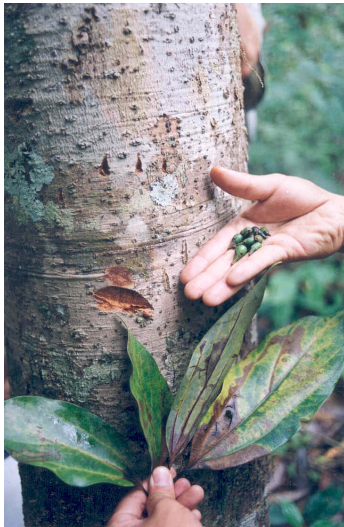# Bear fruits in Semi-evergreen Forest

Ficus sp. Moraceae

Polyalthia viridis
Annonaceae

Cinnamomum sp.
Lauraceae

Lithocarpus truncatus
Fagaceae

Michelia baillonii
Magnoliaceae