Activity patterns of Asiatic black bears (*Ursus thibetanus*) in the Central Mountains of Taiwan

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Abstract

Shifts in activity patterns and time budgets in response to environmental variables may yield insights into key factors affecting animal life histories. Activity data on wild Asiatic black bears *Ursus thibetanus* are limited, and non-existent in tropical portions of their geographic range. During November 1998–November 2000, we monitored the activity (active vs. inactive) of bears within a national park in the tropics of central Taiwan. On the basis of 4630 readings from motion-sensitive transmitters obtained in 24-h monitoring sessions, bears were active 54–57% of the time over the course of the year. However, bears were more active during summer $(60 \pm 15\%$ SD) and fall $(60 \pm 15\%)$ than in spring $(47 \pm 13\%)$. They were active mainly during daylight hours in spring and summer, and also during fall when acorns, a principal fall food, were scarce. However, extensive nocturnal activity occurred in fall when acorns were abundant. Increased nocturnal activity in fall is consistent with studies of the related American black bear *Ursus americanus*, and suggests that this behavior is not necessarily driven by preparation for winter denning or because of disturbance by hunters (as posited in previous studies), as bears in our study did not den (except parturient females) and were not hunted or otherwise disturbed by people.

Introduction

Animals may adapt to changing daylength, weather and food supplies by altering their daily pattern of activity (Aschoff, 1964; Nielsen, 1983; Halle, 2000). Variations in activity patterns and time budgets may also occur in response to competitors, prey, threats or other disturbances (Ayres, Chow & Graber, 1986; Olson, Squibb & Gilbert, 1998; Laundré, Hernández & Altendorf, 2001; Neale & Sacks, 2001). As such, activities and time budgets may yield insights into some of the key factors that ultimately affect life histories (Bunnell & Harestad, 1990) and may thus be important to the development of conservation plans for imperiled species.

Life histories of bears are highly variable both among and within species, related to their expansive geographic distributions and the multitude of habitats that they occupy (Garshelis, 2004). The Asiatic black bear *Ursus thibetanus* ranges north to south from Russia to southern Thailand, and east to west from Japan to Iran (Servheen, Herrero & Peyton, 1999). However, detailed studies of this species have been limited to a small portion of this range, all in north-temperate environments ($>30°$N, mainly Russia, Japan, and a small portion of China).

We studied Asiatic black bears in a tropical setting, although with several of the same primary food resources found in temperate systems, especially oaks, which produce a principal food for bears in many ecosystems (Mattson,

1998; Vaughan, 2002; Hashimoto *et al.*, 2003; Huygens *et al.*, 2003). It was not possible to assess directly the effects of environmental factors on reproduction or mortality of bears in this area, as these animals occurred at low density, could rarely be observed, and were difficult to catch and radiolocate over the large areas in which they resided. Indeed their continued existence in our study site in central Taiwan was largely attributable to the impediments to human access posed by the steep terrain and a paucity of foot trails. Instead, we chose to monitor bear activities, which could be accomplished just by listening to signals of radio-collared animals from various locations, and to evaluate some environmental factors potentially affecting these bears.

Sighting reports by people in the field suggested that bears in Taiwan (so-called Formosan black bears *Ursus thibetanus formosanus*) were active both during day and night (Wang, 1990). Conversely, observations of captive bears indicated that they were active mainly diurnally, with peaks at dusk and dawn (Wang, 1990; Hwang & Wang, 1993). The latter pattern may have been influenced by the captive situation and human activities (e.g. feeding times); however, this same pattern has been commonly reported for other species of bears in the wild (reviewed by Paisley & Garshelis, 2006). In the only studies of activity patterns of wild Asiatic black bears, Schaller *et al.* (1989) and Reid *et al.* (1991) found that four radiocollared individuals in central China were principally diurnal.

This was the first telemetry study of Asiatic black bears in a tropical environment, the Central Mountains of Taiwan. Despite being tropical, the area is not aseasonal; food availability for bears varies seasonally and yearly (Hwang, Garshelis & Wang, 2002). We hypothesized that Formosan black bears would, like temperate bears, adapt to seasonally changing food supplies by varying both the amount of time spent foraging and the timing of peak activity. Specifically, we posited that increased food abundance would prompt increased activity, as bears in general tend to be 'energy maximizers,' responding to plentiful foods by eating more rather than eating a fixed amount and resting more (Paisley & Garshelis, 2006). However, whereas Formosan bears have access to the same sorts of fat-rich foods (primarily acorns) as temperate bears, anecdotal evidence suggested that these bears did not hibernate; thus, with less need to accumulate large fat reserves, they may have been less 'hyperphagic' (Nelson *et al.*, 1983). We also hypothesized that because our study area, within a national park, had little human activity, bears would maintain a basically diurnal activity rhythm. Previous studies of bears of several species suggested that nocturnal activity is primarily a consequence of human disturbance (Roth, 1980; Ayres *et al.*, 1986; Griffiths & van Schaik, 1993; Olson *et al.*, 1998; Beckmann & Berger, 2003; Bridges, Vaughan & Klenzendorf, 2004).

Materials and methods

Study area

Our study site in Yushan National Park (YNP), Taiwan, was located just south of the Tropic of Cancer (23°19′N, 121°10′E). This park comprised 1055 km^2 of Taiwan's Central Mountain Range. The focal point of our study was in southeastern YNP in the watershed of the Lakulaku River. Visitors were banned from most of this area, which is administratively designated an ecologically protected area. There was little human activity other than routine maintenance to the single trail into the area.

The average annual rainfall in YNP was 300–470 cm. The monsoon season occurred during May–October, with typhoons most prevalent during July–September. Yearly average temperatures of 20, 10 and 5 °C corresponded to the 1000, 2500 and 3500 m elevational contours, respectively (data from YNP). Snow generally occurred at elevations > 3500 m during December–April. The monthly mean daily temperature for our study area at 500 m elevation was warmest in July (24 °C) and coldest in January and February (14 °C). Six principal plant zones corresponded with elevational bands: broadleaf forest (300–1800 m, dominated by Lauraceae and Fagaceae), *Chamaecyparis formosensis* (1800–2500 m), *Tsuga chinensis* (2500–3000 m), *Abies kawakamii* (3000–3500 m), subalpine shrub (> 3500 m) and an alpine herbaceous zone (> 3800 m; Chen, 1989).

We defined three seasons based on plant phenology and shifts in bear food habits (Hwang *et al.*, 2002): spring (February–May), summer (June–September) and fall (October–January). Bears in our study area mainly consumed succulent vegetation in spring, soft fruits (e.g. *Machilus*) in summer and hard mast (e.g. acorns, mainly *Cyclobalanopsis* spp. and *Quercus* spp., and walnut *Juglans cathayensis*) in fall. Our efforts in fall focused within a once-settled hillside, Daphan, which was a 3-day hike (40 km) from the park entrance. This area was dominated by ring-cupped oaks *Cyclobalanopsis glauca* and Asiatic pines *Pinus taiwanensis*.

Radiocollaring and activity monitoring

We captured bears with Aldrich spring-activated foot snares in cubby sets (Johnson & Pelton, 1980) or in a barrel trap during 1998–2000. We immobilized captured bears using a blowpipe dart with a mixture of ketamine (4–5 mg kg^{-1} estimated body mass) and xylazine (2 mg kg^{-1}). Once tractable, bears were weighed, ear tagged and measured. An upper first premolar was taken from each bear for estimation of age based on counts of cementum annuli in stained sections (Willey, 1974). Bears ≥ 4 years old were considered adults. Following completion of animal handling, we injected yohimbine (2 mg kg^{-1} estimated body mass) intravenously as an antagonist to xylazine and released bears at the capture site.

We fitted bears with either conventional very high frequency (VHF) radiocollars (164–166 MHz; Advanced Telemetry Systems, Isanti, MN, USA) or satellite-based transmitters [global positioning system or platform transmitter terminal (PTT)] that were also equipped with a VHF transmitter (Advanced Telemetry System; Televilt International AB, Lindesberg, Sweden; North Star Science and Technology, Baltimore, MD, USA). Each radiocollar contained a leather breakaway link to enable it to drop off the bear's neck after about 1–2 years (Garshelis & McLaughlin, 1998).

Activity data were interpreted from signals of VHF transmitters containing a motion-sensitive device that increased the pulse rate from a base rate of 65 ppm up to nearly 200 ppm in response to movements of the animal's head. Paisley & Garshelis (2006) used the same type of transmitters on Andean bears *Tremarctos ornatus* and, through visual observations of radiocollared individuals, developed criteria to separate activity from inactivity based on the pulse rate of the transmitter. We used similar criteria to categorize signals as inactive (< 68 ppm), active (> 75 ppm) or uncertain (68–75 ppm). For two bears with transmitters lacking a motion-sensitive device, we categorized activity by the integrity of the radiosignal (erratic = active, steady = inactive, slight fluctuation = uncertain). Before using this technique, we tested it with radiocollars that were not on bears (as did Roth & Huber, 1986) and were satisfied that it yielded reliable results. Moreover, although these data were collected differently, the levels and patterns of activity of these two bears were similar to bears with activity-sensing collars.

Activity samplings (readings) were obtained by listening to radiosignals for 3 min at each half-hour interval over a period of 24 h (i.e. diel). Another 3-min period of signal monitoring was added if we were uncertain of the animal's

activity. We attempted to conduct up to three diel monitoring sessions each month on each animal within range of the ground telemetry equipment.

Assessment of food production

We observed and recorded annual and seasonal changes in availability and distribution of important bear foods. Because acorns were the dominant item in fall scats (Hwang *et al.*, 2002), we paid particular attention to productivity of this food. We subjectively rated acorn production of the predominant oak species (ring-cupped oak and Arishan oak *Quercus stenophylloides*) as abundant, moderate or poor based on the number of nuts observed on trees. Subjective ratings of fruit abundance in other studies have been useful in comparing habitats used by bears and explaining variations in bear behavior (Noyce & Coy, 1990; Noyce & Garshelis, 1997).

Data analysis

We calculated the proportion of readings categorized as active during each hourly increment (e.g. 1200–1300) for each bear each month. A mixed-model factorial analysis of variance was used to test for differences in the hourly probability of activity each month due to temporal (e.g. time of day and season) and individual effects and their interactions using program MacAnova (Oehlert & Bingham, 2002). In the model, individual bear was considered a random factor.

Seasonal activity rhythms were estimated by pooling data from all bears for each month and calculating the proportion of active readings within each hourly increment. These monthly averages were combined to produce seasonal averages.

We estimated total time active per day (time budgets) using only 24-h monitoring sessions with at least 43 of the 48 (90%) possible half-hour activity readings. The proportion of time active per day was estimated by considering each 24-h monitoring session as a sampling unit. We used published times of sunrise and sunset to distinguish diurnal and nocturnal periods. To test whether diel, diurnal and nocturnal activity patterns varied among seasons, we averaged the proportion of time active among individual bears and made pairwise comparisons with two-tailed *t*-tests after testing for equal variances.

During activity monitoring sessions, radiosignals sometimes faded and disappeared. This occurred either because bears moved out of signal reception range or because they slept and their location and body position reduced the range of the transmitter. When this occurred, we moved our position in an attempt to receive the signal. If we could not regain the signal, and if the loss was associated with the bear sleeping, then our data would be biased toward activity. To account for this, we performed an analysis whereby missing data occurring within an apparent rest period (i.e. the bear's estimated location was unchanged when the signal was regained) were counted as inactive.

Results

We caught 14 bears (12 males, two females) at Daphan during the fall and one male during summer in an area 3 km from Daphan. We captured six bears (116 trapnights/capture) in 1998, one bear (967 trapnights) in 1999 and seven bears (57 trapnights/capture) in 2000. Capture success was related to food conditions. In 1998, acorn production by ring-cupped oaks in Daphan was abundant and widespread, covering an area $>12 \, km^2$. This supported a high density of bears (based on telemetry data and observance of fresh signs) for about 7 weeks. In 1999, acorn production in Daphan was poor; hence this area attracted few bears. In 2000, the acorn crop in Daphan was abundant but concentrated in a small ($<2 \, km^2$) patch, which was depleted in about 2 weeks by an apparent high density of foraging bears.

We obtained 4630 activity readings on 12 bears during November 1998–November 2000. The probability of hourly activity was influenced by time of day, and interactions between individual bears, time of day and season ($P \leq 0.01$, mixed-model ANOVA table in Hwang, 2003). During the fall season, most variation in activity was explained by differences among individuals, year, and the interaction between individuals and time of day ($P < 0.005$).

Bears were active during all months; they did not den during winter (therefore, winter was not regarded as a distinct season). However, an adult female with a PTT collar was lost from both VHF and PTT contact during mid-February–May 2000, and then abruptly reappeared. We suspect that this was related to her occupying a birthing den that blocked radiotransmission. In November 2000 we observed this bear and, although we did not see cubs, she made a soft cooing sound, which suggested she was calling her cubs.

Averaged over all seasons and hours, bears were active $57 \pm 15\%$ (sd) of the time (range = 15–88% active per day, $n = 73$, 24-h monitoring sessions). Diel activity levels did not vary among bears ($F_{6,64} = 1.75$, $P = 0.147$) or between sexes (59% males vs. 52% females; $F_{1,69} = 2.20$, $P = 0.142$), but differed by season ($F_{2,71} = 5.94$, $P = 0.004$). Diel activity in spring ($47 \pm 13\%$, $n = 16$) was lower than in summer ($60 \pm 12\%$, $n = 10$, $t = 2.66$, $P = 0.01$) and fall ($60 \pm 15\%$, $n = 47$, $t = 3.31$, $P = 0.002$; Fig. 1). During fall (when we had the most data), no differences were detected among diel time budgets of individuals (range: 56–74%; $F_{6,36} = 1.8$, $P = 0.13$), sexes ($\bar{x} = 64 \pm 10\%$ males vs. $60 \pm 8\%$ females; $t = 1.12$, $P = 0.23$) or age groups ($64 \pm 10\%$ adults vs. $61 \pm 8\%$ subadults; $t = 0.39$, $P = 0.70$).

In the foregoing analyses we did not include radiosignals that disappeared during a bear's apparent rest period. By counting such periods of signal loss as inactivity, the overall active time budget was $54 \pm 17\%$, which was not different from the result excluding these adjustments, overall ($F_{1,150} = 1.86$, $P = 0.175$) or for any season (Fig. 1).

Over all seasons, bears were more active during daylight hours ($67 \pm 25\%$, $n = 88$ days) than at night ($45 \pm 28\%$, $n = 77$ nights, $t = 5.17$, $P < 0.001$). The probability of activity differed among individuals during daylight hours (range:
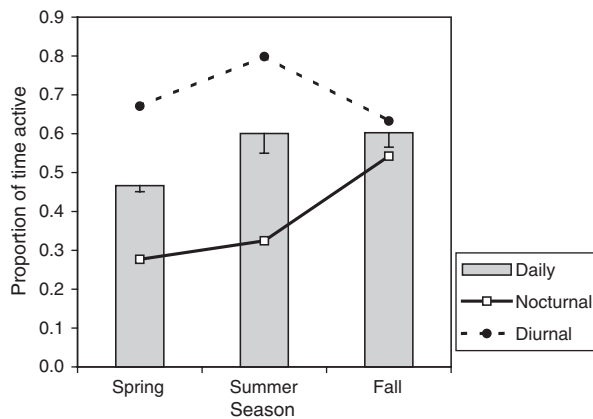
Figure 1 Seasonal diel (24-h) levels of activity (bars), and separate diurnal and nocturnal activity levels (lines) of Asiatic black bears *Ursus thibetanus* in Yushan National Park, Taiwan, 1998–2000. Error bars indicate the activity levels if missing signals during rest periods were counted as inactive.
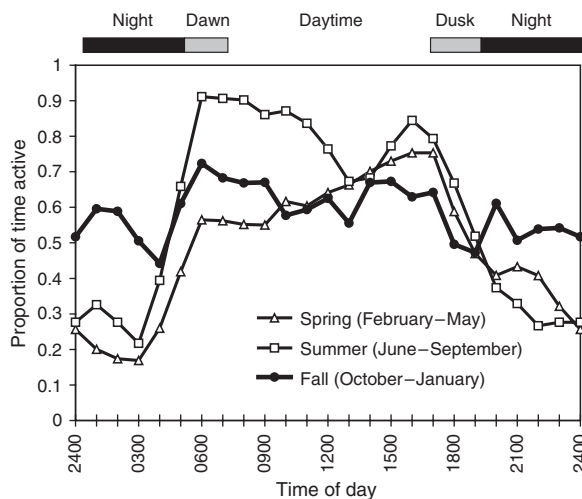

Figure 2 Seasonal variation in daily activity patterns of Asiatic black bears *Ursus thibetanus* in Yushan National Park, Taiwan, 1998–2000.

Figure 3 Activity patterns of an adult male bear radiotracked during the non-oak season (April–June 1999) and two oak (fall) seasons (October–January) in Yushan National Park, Taiwan, showing apparent effects of an abundant acorn crop in 1998 versus a poor crop in 1999.

41–91%; $F_{6,38} = 4.1$, $P = 0.003$), but not at night (range: 38–75%; $F_{6,34} = 1.8$, $P = 0.14$).

In summer and spring, onset and cessation of activity occurred near sunrise and sunset, respectively (Fig. 2). During these seasons, bears were more active during day than at night (spring $t = 6.1$, d.f. = 34; summer $t = 5.2$, d.f. = 22; both $P < 0.001$; Fig. 1). In fall, activity was more consistent throughout daytime and nighttime hours (range: 44–72% active); no difference was observed between diurnal and nocturnal activity ($t = 1.71$, d.f. = 103, $P = 0.09$; Fig. 1). Nocturnal activity in fall ($54 \pm 27\%$, $n = 49$ full nights of monitoring) was significantly greater than during summer ($32 \pm 29\%$, $n = 11$, $t = 2.38$, $P = 0.013$) and spring ($28 \pm 18\%$, $n = 17$, $t = 3.73$, $P < 0.001$). Conversely, diurnal activity was greater in summer ($80 \pm 15\%$, $n = 13$) than in fall ($63 \pm 27\%$, $n = 56$, $t = 2.13$, $P = 0.037$).
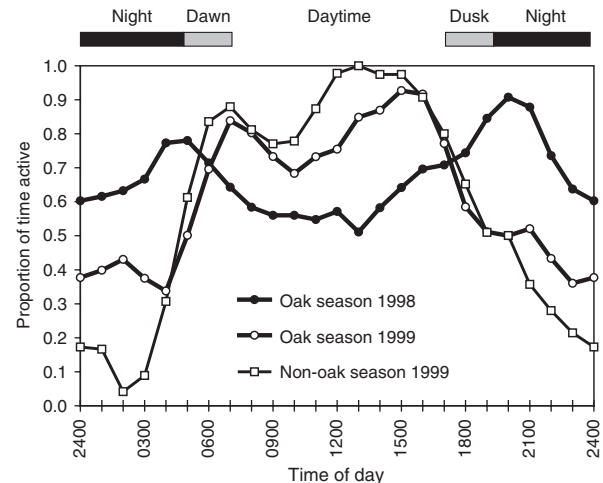
In fall 1998, bears maintained a high activity level both during the daytime ($\bar{x} = 62 \pm 26\%$, $n = 31$) and at night ($\bar{x} = 70 \pm 17\%$, $n = 29$, $t = 1.52$, $P = 0.13$). The only radio-collared female bear in Daphan was more nocturnally oriented (74% active at night, 41% during the day) than the males. In fall 1999, by contrast, bears were more active during the day than at night ($83 \pm 13\%$, $n = 16$ vs. $44 \pm 15\%$, $n = 13$, $t = 7.42$, $P < 0.001$). In fall 1999, bears were more active diurnally ($t = 3.12$, $P = 0.003$) and less active at night ($t = 4.69$, $P < 0.001$) than they were in 1998. The mean diel activity level of five bears in fall 1998 was higher than that of two bears monitored in fall 1999 ($66 \pm 8\%$, $n = 28$ diels vs. $59 \pm 12\%$, $n = 15$, $t = 2.11$, $P = 0.04$), consistent with our hypothesis that they would spend more time feeding when food was more plentiful.

Only one bear (an adult male) was radiomonitored in Daphan during two different years. During April–June 1999 this bear was active $56 \pm 7\%$ ($n = 3$ diel monitoring sessions) of the time, primarily during daylight hours (Fig. 3). Peak activity occurred 1–2 h before sunrise and 1–3 h after sunset. This activity rhythm continued into the fall of that year. This pattern differed from his activity the previous fall, when his diel activity level was higher ($\bar{x} = 67 \pm 6\%$ in 1998, $n = 7$ vs. $58 \pm 12\%$ in 1999, $n = 14$, $t = 2.10$, $P = 0.05$) and he was more active at night but less active during day.

Discussion

The mainly diurnal activity pattern of Asiatic black bears monitored in our study was consistent with the results of previous studies of this species (in China: Schaller *et al.*, 1989; Reid *et al.*, 1991) as well as studies of other bear species in places with little human activity. These include

American black bears (Garshelis & Pelton, 1980; Ayres *et al.*, 1986; Lariviére, Huot & Samson, 1994; Maehr, 1997; Holm, Lindzey & Moody, 1999; Beckmann & Berger, 2003), Andean bears (Paisley & Garshelis, 2006), sun bears *Helarctos malayanus* (Griffiths & van Schaik, 1993; Wong, Servheen & Ambu, 2004) and some populations of brown/grizzly bears *Ursus arctos* (Stelmock & Dean, 1986; MacHutchon, 2001).

Similar to other tropical bears (Andean bears, sun bears and sloth bears *Melursus ursinus*), bears in our study were active during all months, including winter. This conclusion was based not just on the radiocollared bears that we tracked, but also on fresh signs that we observed and sighting reports by staff, visitors and indigenous locals of YNP (Hwang, 2003). This behavior differs from Asiatic black bears in temperate areas (31–50°N), where they den during winter (Hazumi & Maruyama, 1987; Reid *et al.*, 1991; Huygens *et al.*, 2001; Seryodkin *et al.*, 2003). Parturient females, however, are obligated to den in all latitudes because they produce altricial young, as we suspected for one adult female whose radio signal was lost during mid-February–May 2000. This period coincides with limited data on the timing of denning for parturient Asiatic black bears (I. Seryodkin, pers. comm.). A den site underground or in a hollow tree, as observed elsewhere for this species (Li *et al.*, 1994; Seryodkin *et al.*, 2003), would block PTT signals to satellites.

After emerging from winter dens, black bears in North America generally have a low level of activity, which gradually builds through late spring and summer, with increasing supplies of carbohydrate-rich fruits (Amstrup & Beecham, 1976; Garshelis & Pelton, 1980; Swanson, 1990). We observed this same seasonal pattern (Fig. 1), even though bears in our study did not den in winter. This differed from results in Sichuan, China, where Asiatic black bear activity was high in spring (May–June, 63%; although this was more than a month after they emerged from dens) and summer (July–August, 62%), but then declined in fall (September–October, 57%; Reid *et al.*, 1991). Habitat, topography and foods were similar for Sichuan and YNP; therefore, observed seasonal differences in activity may have been an artifact of small sample sizes ($n = 2$ bears in Sichuan) or due to phenological differences or yearly effects.

The overall yearly level of activity that we observed for tropical Asiatic black bears (54–57%, depending on whether fading signals during apparent rest periods were considered missing data or inactivity) fits well within the range observed for other species of bears (population means generally 50–60%; summarized by Paisley & Garshelis, 2006). Likewise, Wu (2004) continued to monitor two of our radiocollared bears during January–July 2001 and observed 48% activity ($n = 15$ days) for one and 55% activity ($n = 18$ days) for the other.

Formosan black bears maintained a high activity level in fall, but were more nocturnal than in spring and summer. A shift from diurnal or crepuscular activity in spring and summer to increased nocturnal activity in fall has been reported elsewhere for both Asiatic (Reid *et al.*, 1991) and American black bears (Garshelis & Pelton, 1980) and has

often been attributed to either increased foraging in preparation for winter denning (Nelson *et al.*, 1983; although daily time budgets did not increase) or avoidance of diurnal disturbance or threats by humans (e.g. hunters: Swanson, 1990; Bridges *et al.*, 2004). However, as bears in our study did not hibernate, nor were they threatened or disturbed by humans, we had hypothesized that they would maintain a diurnal activity pattern. It appears that their shift to more nocturnal fall activity during an abundant mast year must have been adaptive for other reasons. This finding also suggests that a common explanation for this behavior should be sought that fits bears that hibernate as well as those that do not, and those that are hunted in fall as well as those that are not.

We suggest three non-mutually exclusive reasons for increased nocturnal foraging during the fall. First, densely clumped foods in fall may make it easier for bears to feed at night. In places where American black bears did not resort to increased nocturnal foraging in fall, they either did not feed on acorns (Amstrup & Beecham, 1976; Lariviére *et al.*, 1994) or did so minimally (Maehr, 1997); however, they sometimes became more nocturnal in fall even in areas where acorns were not a major food source but where other clumped sources of hard mast [e.g. hazelnuts (*Corylus* sp.)] were available (Swanson, 1990). Second, nocturnal activity may be a thermoregulatory-energetic adaptation to greatly increased body fat, especially in years when hard mast (rich in fat) was prevalent. Third, when feeding on clumped foods, gut capacity may be filled in a short time, necessitating more frequent interruptions of feeding bouts, resulting in a more uniform distribution (but lower level) of feeding activity throughout the day. The habitat for American black bears in south-eastern United States, which is similar to that in our study area, produces nearly an order of magnitude more food (measured in terms of available calories) during the fall oak season than during the summer berry-producing season (Inman & Pelton, 2002), and bears there switched to a more uniform activity pattern when acorns became available (Garshelis & Pelton, 1980).

On the basis of foraging theory, animals either spend the minimum time feeding until satiated or try to maximize energy intake to increase their fitness (Schoener, 1971). Paisley & Garshelis (2006) proposed that Andean bears, which also do not hibernate, used an energy-maximizing strategy, and our data on Asiatic black bears support this conclusion. In our study, when acorns were concentrated and abundant, bears were more active (presumably feeding more) than when acorns were not abundant and they had to seek other, more dispersed sources of food during the fall (Hwang *et al.*, 2002). Likewise, Lariviére *et al.* (1994) reported that American black bears maintained a higher level of fall activity in a year when beechnuts *Fagus grandifolia* were abundant, compared with a year when they were not.

Our capture data and observations of signs (scats and tree limbs broken by feeding bears) during three fall seasons suggested that bear density at Daphan was higher during years with relatively abundant acorn production (1998 and 2000) than when acorns were scarce (1999). Although

capture success is also affected by bears' attraction to bait, we would have expected bears to be more attracted to bait when natural food was scarce; therefore, low capture success and hardly any evident bear signs in 1999 were likely reliable indicators of few bears being in the Daphan area that year. In all years, it appeared that few females occupied this area; moreover, the only two radiocollared females that did so had a more nocturnal activity pattern than the males or moved away from the most productive acorn patch (Hwang, 2003), suggesting both a temporal and spatial avoidance of the male congregation by females. Other studies also reported that among both Asiatic and American black bears, females avoided rich oak feeding areas occupied by male bears (Garshelis & Pelton, 1981; Huygens & Hayashi, 2001).

Although we identified several similarities and some differences between Asiatic black bears in this tropical setting and bears of this and related species elsewhere, activity data are still too scant for other areas in the range of this bear to make further comparisons. We present these data more as a starting point in understanding the behavior of this species. We also attempted to track the movements of these bears, but their wide travels into inaccessible areas greatly hindered collection of these data. In such circumstances, which we believe are common in many of the remote, remnant populations of this species, studies of activity may be more suitable. We suggest that combined activity–food habits studies in portions of the range where acorns are unavailable and/or where Asiatic black bears are sympatric with sun bears (south-east Asia) would be particularly instructive in terms of comprehending the breadth of this species' life-history adaptations.

Acknowledgements

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