# Home ranges of Asiatic black bears in the Central Mountains of Taiwan: Gauging whether a reserve is big enough

**Mei-Hsiu Hwang[1,5], David L. Garshelis[2,6], Yu-Hui Wu[3], and Ying Wang[4]**

[1]*Institute of Wildlife Conservation, National Pingtung University of Science and Technology, 1 Hsech-Fu Road, Nei-Pu, Pingtung, 91201, Taiwan*
[2]*Minnesota Department of Natural Resources, Grand Rapids, MN 55744, USA*
[3]*Institute of Natural Resources, National Dong Hwa University, Shoufeng, Hualien, Taiwan*
[4]*Department of Life Science-National Taiwan Normal University, Taipei, Taiwan*

***Abstract:*** Asiatic black bears (*Ursus thibetanus*) are threatened by habitat loss and poaching, especially in the tropical portions of their range; reserves serve a crucial role in conserving this species. Yet data on spatial and habitat requirements for this species in tropical areas, necessary for assessing the efficacy of reserves, is virtually nonexistent. We used mainly ground-based telemetry to investigate home range sizes of the endangered Formosan subspecies (*U. t. formosanus*) in the largest park in Taiwan. The largest observed home range (117 $km^2$) was an adult female with a satellite radiocollar. Normally, male bears have significantly larger home ranges, but males tracked with ground telemetry often could not be located due to the rugged terrain and limited accessibility of our study area, so their home ranges were underestimated. This is a common, but often neglected problem of telemetry studies in protected areas with difficult human access. Although elevations ranged from 300 to >3,500 m, bears mainly used areas below 2,000 m, selecting broadleaved and mixed broadleaved–coniferous forests. Production of acorns (*Cyclobalanopsis* and *Quercus*), a sought-after fall food, varied yearly. One site in the interior of the park produced an abundance of acorns in some years, attracting a dense congregation of bears; however, females and subadult males were socially excluded. Despite limitations of our telemetry data, we observed that half the bears, all caught near the center of the park, traveled beyond the boundaries where they were more vulnerable to illegal hunting, suggesting that more protection is needed along the edges of the park.

***Key words:*** acorn production, Formosan black bear, habitat use, reserve size, spatial requirements, telemetry sampling bias, *Ursus thibetanus formosanus*

***Ursus 21(1):81–96 (2010)***

Protected areas serve as sanctuaries and the primary tool for conservation in the tropics (Kramer et al. 1997, Terborgh et al. 2002). Establishment of protected areas for threatened species requires knowledge of the spatial and habitat requirements of those species. Protected areas are often established in places with low human density, owing to difficult access as a result of rugged terrain and lack of roads. Hence, the very attributes that help protect wildlife also make it difficult for researchers to conduct studies there.

For wide-ranging large mammals, radiotelemetry has been instrumental for obtaining data on space and habitat use. A large disparity exists, though, in the number of telemetry studies that have been conducted on different species, even among large mammals within the same taxa. Among the 8 species of bears (Ursidae), for example, 2 species, the American black bear (*Ursus americanus*) and brown bear (*U. arctos*), have been investigated extensively, with more than 30 published studies of annual home range size on each (Garshelis 2004), plus many more studies of seasonal home ranges and short-term movements. Studies of polar bear (*U. maritimus*) movements pose numerous logistical constraints, yet more than 10 extensive home range studies, most employing satellite telemetry, have been conducted on this species (Garshelis 2004, Parks et al. 2006). The other 5 bear species, all listed as either

[5]hwangmh@mail.npust.edu.tw [6]dave.garshelis@state.mn.us

endangered or vulnerable (IUCN 2009), have been studied much less. These species are all endemic to either Asia or South America, where funding, logistical constraints, administrative constraints (e.g., permit restrictions), and to some extent lack of adequate training have hampered telemetry studies, especially in the tropics and subtropics.

That more is known about bear ecology in temperate than tropical areas stands in contrast to information needs: in most tropical areas, bear habitat is diminishing (Servheen et al. 1999, Japan Bear Network 2006). Habitat reduction, combined with unsustainable levels of human exploitation, has put many populations at risk (IUCN 2009). The size of protected areas, however, is a limiting factor for many species, especially those as wide-ranging as bears (Powell et al. 1996, Beringer et al. 1998, Woodroffe and Ginsberg 1998, Woodroffe 2001, Wielgus 2002). Hence, the paucity of information on bear movements and home ranges south of the temperate region is a detriment to the establishment of adequate-sized protected areas, and thus a limitation to bear conservation.

Our study subject was the Asiatic black bear (*U. thibetanus*), one of the largest carnivores in Asia. Studies of movements and home ranges of Asiatic black bears have been few, often with small sample sizes, and limited to temperate portions of their geographic range (China: Schaller et al. 1989, Reid et al. 1991; Japan: Hazumi and Maruyama 1986 and 1987, Ohsako 1995, Izumiyama and Shiraishi 2004; Russia: Kostyria et al. 2002). This species inhabits remnant patches of forest within what was once an expansive contiguous geographic range (Servheen et al. 1999). The fact that they have persisted mainly in areas where physical barriers have impeded human intrusion speaks to the difficulties of data collection. These logistical constraints largely explain the limited success of past studies of their home range and habitat use.

Although satellite telemetry has been used for tracking other highly mobile bear species, and GPS (global positioning system) collars have recently been used on Asiatic black bears to study their activity (Yamazaki et al. 2008), previous studies of home ranges of this species have not employed these techniques. We used aerial, satellite, and GPS telemetry, as well as standard ground telemetry to examine home range and habitat use of a subspecies known as the Formosan black bear (*U. t. formosanus*) in a rugged, mountainous protected area in central Taiwan (Fig. 1). Formosan black bears are an endangered endemic of Taiwan. Like Asiatic black bears elsewhere in Eastern and Southeastern Asia, they are threatened by limited habitat and uncontrolled poaching for their parts (e.g., gall bladders, paws, and meat; Japan Bear Network 2006).

We hypothesized, based on previous studies of this species as well as the ecologically similar American black bear (Garshelis and Pelton 1981, Beck 1991, Reid et al. 1991, Izumiyama and Shiraishi 2004), that Formosan black bears would exploit the large elevational gradient in this mountainous area to locate seasonally varying food supplies. We further hypothesized that the topographically and vegetatively diverse habitats would help insulate these bears within the largest protected area in Taiwan: given that previous estimates of home range size for this species in similar mountainous environments were ~3–10% of the size of this reserve, we expected that bears captured well into the interior of the reserve would not venture outside, and thus would be at minimal risk from poaching. Accordingly, we also sought to assess the utility of ground telemetry for evaluating the efficacy of a reserve for conserving bears.

## Study area

Our study area in Yushan National Park (YNP), Taiwan, was located just south of the Tropic of Cancer (23°19′ N, 121°10′ E), within the heart of the Central Mountain Range. Established in 1985, YNP comprises 1,055 km$^2$. Our study was focused in southeastern YNP in the watershed of the Lakulaku River, designated an ecological protected area. Routine maintenance to the single trail into the area was the only human activity other than ours during this study. We chose YNP, and this study area within YNP, because of reasonable logistical access, known presence (concentration) of bears, and administrative and financial support provided by the park.

Two-thirds of YNP lies above 2,000 m in elevation (range: 300–3,952 m), and >30 mountain peaks exceed 3,000 m. Average annual rainfall was 3,000–5,000 mm, varying with elevation. Monsoon rains occurred during May–October. Relative humidity was generally high (80–93%) throughout the year. Average annual temperatures of 20°C, 10°C and 5°C corresponded to the 1,000-, 2,500-, and 3,500-m

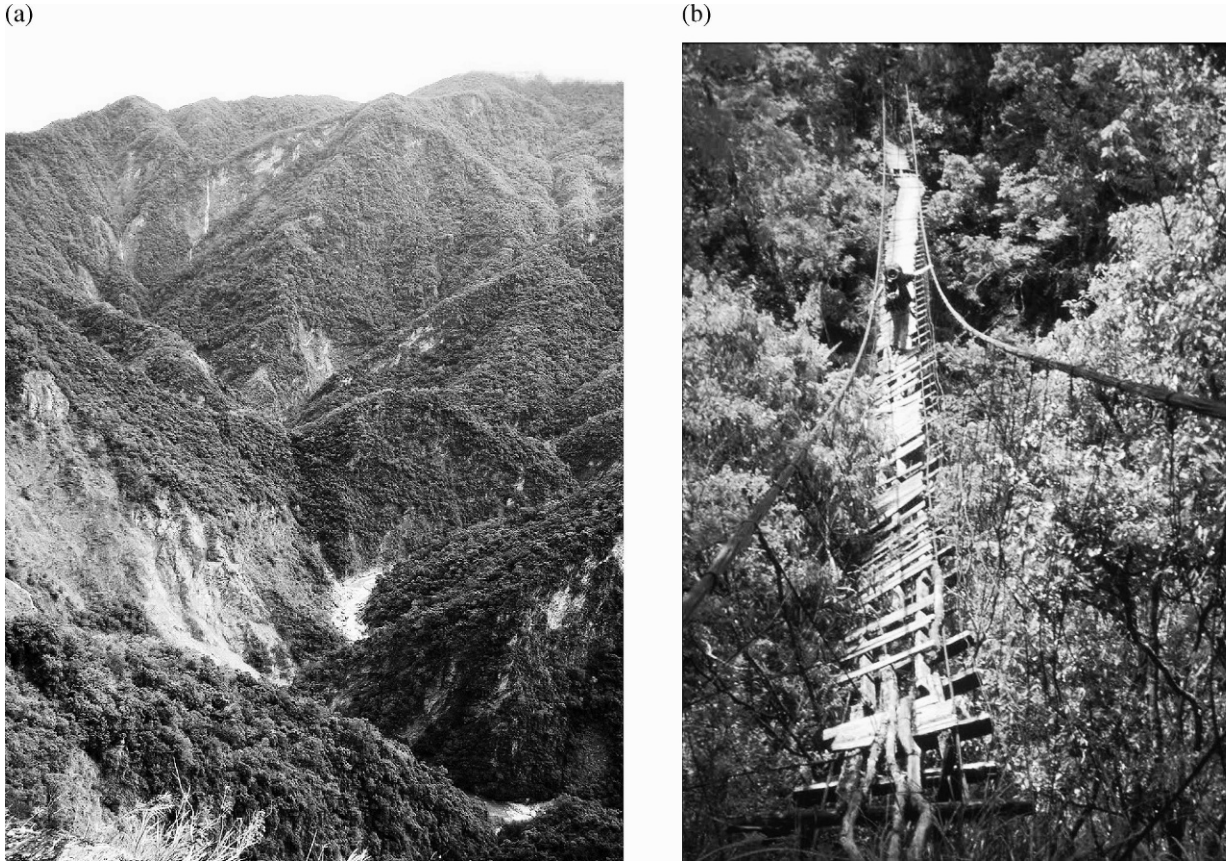


**Fig. 1. Rugged terrain (a) and difficult human access (b) in our study site in central Taiwan are typical of many protected areas where Asiatic black bear populations exist.**

elevational contours, respectively (data from YNP). At the elevational extremes, July temperatures averaged 24°C at 500 m, whereas above 3,500 m, snow occurred during December–April.

Vegetation varied sharply with latitude. Six principal vegetation types were categorized by dominant genera (Su 1984): *Ficus–Machilus* zone (<500 m, foothill), *Machilus–Castanopsis* (500–1,500 m, submontane), *Quercus* (1,500–2,500 m, montane), *Tsuga–Picea* (2,500–3,100 m, upper montane), *Abies* (3,100–3,600 m, subalpine), and alpine (>3,600 m). We captured bears mainly during the fall in an oak-dominated area at 1,100–1,600 m elevation. This area, called Daphan, is 40 km from the park entrance and a 3-day hike along a partially-maintained trail (Fig. 1). Possibly because of past human settlement in this area, it appears to be unique within YNP in terms of an extraordinarily high concentration of ring-cupped oaks (*Cyclobalanopsis glauca*).

## Methods

### *Trapping and radiotracking*

We captured bears during 1998–2000 using Aldrich spring-activated foot snares and barrel traps. Captured bears were immobilized using a blowpipe dart with a mixture of ketamine (4–5 mg/kg estimated body mass) and xylazine (2 mg/kg), then weighed, ear-tagged, radiocollared, and measured. An upper first premolar was extracted for estimation of age based on counts of cementum annuli in stained sections (Wiley 1974). Bears ⩾4 years old were considered adults. We injected yohimbine (2 mg/kg estimated body mass) intravenously to reverse the anesthesia and released bears at the capture site.

We used conventional VHF (very high frequency) radiocollars (164–166 MHz; Advanced Telemetry System [ATS], Isanti, Minnesota, USA) or satellite-based collars with GPS (ATS, and Televilt International AB [now Followit AB], Lindesberg, Sweden),

PTT (platform transmitter terminal), or GPS-PTT (North Star Science and Technology, Baltimore, Maryland, USA), which also were equipped with a VHF transmitter. Each radiocollar was attached with a leather breakaway link that was designed to drop off the bear's neck after about 1–2 years (Garshelis and McLaughlin 1998).

We radiotracked bears with a hand-held 2-element H-antenna or a 4-element yagi antenna mounted at the Daphan research station and a TR-2 receiver (Telonics, Inc., Mesa, Arizona, USA) during November 1998–January 2002. Radiolocations were determined by the intersection of 2 or more radio-bearings taken simultaneously by observers at 2 locations, or occasionally by a single observer from 2 or more points at an interval of <1 hour. We typically radiotracked along the single trail from the YNP entrance to Daphan. If radio signals of collared bears were not detected, we climbed up high ridges or mountain peaks to search for them.

We plotted bearings on 1:10,000 topographic maps in the field and omitted locations where multiple radio-bearings resulted in a large error polygon. We used only radiolocations with an angle of intersection between 20°–155° (Chu et al. 1989). The mean angle of intersection during our study was 60° (SD = 25).

We radiotracked from a helicopter on 3 occasions to attempt to locate bears that we could not find from the ground. We tracked using 2 H-antennas mounted on the helicopter skids and documented locations with a GPS. Each flight lasted 1–2 hours and covered the entire YNP and neighboring areas.

All 3 GPS collars failed before data could be retrieved. Sporadic data were obtained from 2 PTT satellite transmitters. These had a duty-cycle of 8 hours on (i.e., period of transmission) and 22 hours off, and an expected transmission life of 2 years. Service Argos assigned each satellite location to a location accuracy class (LC; from most to least accurate: 3, 2, 1, 0, A, B, Z). Expected errors were <1 km for LC 1–3, >4 km for LC A, and >10 km for LC B (Rodgers 2001). In actual tests with transmitters placed at known locations in our study area, errors averaged 0.6 km (SD = 0.7) for LC 2 locations to 2.2 km (SD = 2.6) for LC A (Wu 2004); we deemed these errors to be small enough for analysis of home range size. However, LC B errors averaged 19.2 km, which was unacceptably large. Thus, we excluded locations with LC B errors.

### Food ratings

Bears in this area consumed mainly succulent vegetation in spring, soft fruits (e.g., *Machilus*) in summer, and hard mast (e.g., acorns, principally *Cyclobalanopsis* and *Quercus*, and walnut, *Juglans cathayensis*) in fall (Hwang et al. 2002). Bears remained active through the winter (Hwang and Garshelis 2007). We defined 3 seasons based on plant phenology and shifts in bear food habits: spring (Feb–May), summer (Jun–Sep), and fall (Oct–Jan, or oak season). We recorded annual and seasonal changes in availability and distribution of important bear foods, especially acorns, because foods are known to affect bear movements (Rogers 1987, Vaughan 2002, Ryan et al. 2007, Garshelis and Noyce 2008). We qualitatively rated acorn production in Daphan (high, moderate, or low) by observing the number of fruiting trees and amount of ripened fruit on twigs.

### Data analysis

We used radiolocations, locations of capture sites, and locations where collars dropped off to estimate home range sizes. The collection of telemetry locations was often hampered by difficult accessibility and rugged terrain (Fig. 1), resulting in small samples with a biased distribution. Therefore, probabilistic home range models, which assume that the distribution of points is unbiased (Powell 2000), were not appropriate for this dataset. Instead, we used 100% minimum convex polygons (MCP, Hayne 1949).

Our original objective was to estimate home range sizes for bears. However, after experiencing much difficulty in locating them, we modified our objective to simply gauging whether the park was sufficiently large to contain these bears and thereby provide protection from poaching. Thus, small samples of locations per se were not a detriment to this objective so long as we could locate bears when they traveled widely. For calculating home range areas, we excluded bears that were located only within a small area but could not be found when they left that area.

Centers of seasonal home ranges were calculated as the geometric mean of the X and Y coordinates. This is sometimes referred to as an activity center, although we do not use this term because it again suggests that the sampling was unbiased. We calculated home range centers only to provide some quantification of seasonal movements (e.g., Joshi et al. 1995).

**Table 1. Estimated home-range size of Asiatic black bears in Yushan National Park, Taiwan, 1998–2001. Home range size is excluded for bears that were located only within a small area but could not be found when they left that area. Although most are underestimates, these data show that aerial and satellite telemetry were needed to assess actual spatial requirements.**

| Bear ID | Sex–age[a] | Date of capture (mm/dd/yyyy) | Period tracked[b] mm/yyyy | Span (mos.) | Number of locations ($n$ = 241) | | | | MCP[e] ($km^2$) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | Telemetry | | | | |
| | | | | | Ground | Aerial | PTT[c] | Total[d] | |
| 1 | FA | 10/25/1998 | 12/1998–1/1999 | 1 | 7 | | | 8 | |
| 2 | MA | 10/29/1998 | 12/1998–7/2000 | 19 | 24 | 1 | | 26 | 67.2 |
| 3 | MA | 10/31/1998 | 12/1998–7/2000 | 19 | 11 | 3 | | 15 | |
| 4 | MA | 11/02/1998 | 12/1998–3/1999 | 4 | 16 | | | 17 | 43.9 |
| 5 | MS | 11/27/1998 | 11/1998–10/1999 | 11 | 38 | | | 39 | 24.2 |
| 6 | MS | 12/27/1998 | 12/1998–7/2000 | 19 | 6 | 3 | | 10 | 70.8 |
| 7 | FA | 12/09/1999 | 12/1999–11/2000 | 11 | 3 | 1 | 53 | 58 | 117.1 |
| 8 | MA | 08/26/2000 | 8/2000–12/2001 | 16 | | | 16 | 17 | 38.9 |
| 11 | MA | 11/08/2000 | 12/2000–8/2001 | 9 | 24 | | | 25 | 43.8 |
| 13 | MA | 11/13/2000 | 2/2000–9/2001 | 7 | 25 | | | 26 | 24.9 |

[a]FA = female adult; MA = male adult; MS = male subadult.
[b]Period in which locations were obtained, although locations were not obtained in all months.
[c]Includes only locations with ARGOS accuracy codes LC-3, 2, 1, 0, and A.
[d]Includes capture locations.
[e]MCP = minimal convex polygon (100%)

We plotted bear locations on a geographic information system (GIS, ArcGIS 9.2) to estimate use of habitats (i.e., elevation classes and vegetation type). We calculated the proportional area of each habitat type within each home range and also within the overall study area (park boundary with a 5-km buffer strip to account for locations outside). The vegetation map was derived from the third survey for forest resources and land use in Taiwan (Taiwan Forestry Bureau 1995). Habitat parameters of bear locations were obtained from a digital terrain model (DTM) in 40 x 40 m resolution.

We grouped vegetation into 8 types: broadleaved forest, mixed broadleaved–coniferous forest, coniferous forest, meadow–bamboo shrubland, bare-rock (open area), riparian, agricultural land, and other. Elevations were divided in 500-m intervals into 8 zones, ranging from <500 to >3,500 m. We tested for seasonal changes in bear use of different vegetation and elevational zones with two-way ANOVA.

We examined whether bears selected for certain habitat types (i.e., elevation and vegetation) by comparing use to availability, recognizing that availability is difficult to measure, and use, reflected by our radiolocations, could be biased (Garshelis 2000). We used the individual bear, rather than the radiolocation, as the sample unit. We made 2 comparisons: the composition of home ranges compared to the overall study area, and the habitat at point locations compared to the composition of home ranges, which Johnson (1980) referred to as second and third order selection, respectively. Focusing on second-order selection, we used the Chesson selection index (CSI; Chesson 1978, 1983) and 95% confidence intervals (95% CI) to evaluate habitat selection for each bear (e.g., Ratnayeke et al. 2007). Selection was considered significant if the 95% CI did not include the expected CSI value.

## Results

### *Home ranges*

During 2,604 trap nights ($n$ = 195 days) over 3 years, we captured 15 bears (10 adult males, 3 subadult males, 2 adult females) and radiocollared 14. All bears but 1 were caught at Daphan, where bears concentrated during fall.

Four bears, including 2 with VHF collars and 2 with satellite-based collars, left the capture area at Daphan and were never subsequently located. We collected 241 locations for the other 10 bears (Table 1). However, only 8 of these were tracked for an adequate span of time (10–22 months) and yielded a sufficient sample of locations from which to estimate home range size. These yielded MCP estimates of 24.2–117.1 $km^2$ ($\bar{x}$ = 53.8, SD = 30.7, Table 1). Two males tracked from the ground and aerially for ⩾20 months had larger perceived home ranges (67 and 71 $km^2$) than 4 males tracked for 5–

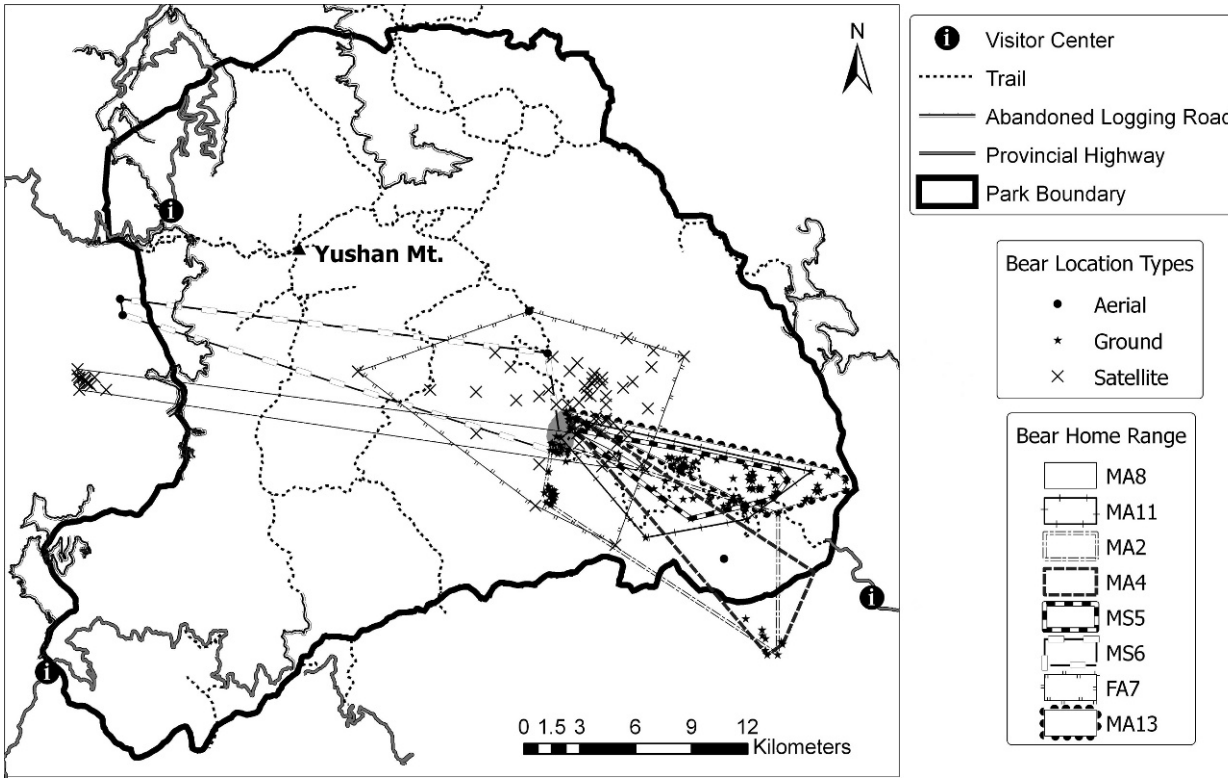


**Fig. 2. Minimum convex polygon (100% MCP) ranges of 7 male (MA: adult; MS: subadult) and 1 female (FA) Asiatic black bear radiotracked in Yushan National Park (YNP), Taiwan, 1998–2001. Radio-locations collected from the ground (including trap sites) generally were near trail or road systems, whereas locations from aerial and satellite tracking were obtained throughout the park and beyond the park boundaries. Gray shaded circle overlaying cluster of points is the capture area, Daphan, where bears congregated in fall, attracted to ring-cupped oak acorns.**

12 months from the ground (24–44 km$^2$). Home ranges of adult ($\bar{x}$ = 44.9, SD = 17.3 km$^2$, $n$ = 4) and subadult males ($\bar{x}$ = 47.5, SD = 32.9 km$^2$, $n$ = 2) tracked from the ground were similar.

Most home ranges were oriented east–west across different watersheds (Fig. 2). Home ranges overlapped extensively among and within sex groups (Fig. 2). We could not test for overlap among centers of activity because locations collected from the ground tended to be clustered near trails and roads from where our tracking was conducted and thus were not truly representative of the utilization patterns of the bears.

A total of 512 PTT readings were obtained for 2 bears (1 M, 1 F; Table 1), but only one-third had latitude–longitude information. Most PTT locational data were in the lower accuracy categories: LC 3 (1.2%), 2 (2.1%), 1 (2.3%), 0 (0.8%), A (7.6%), B (18.6%), and LC Z (invalid data, 67.4%). During the deployed period, the 2 PTTs transmitted for approximately 5,450 hours over a period of 850 days. The average frequency of successful signal transmission was 0.14 and 0.10 transmissions/hour, indicating poor efficiency of these satellite-based transmitters.

The 2 PTT collars produced 53 and 16 useable locations for the adult female (FA7) and male (MA8) bear, respectively, during December 1999–December 2001. The largest home range, 117 km$^2$, was recorded for this female (Table 1). The MCP home range of the male was 39 km$^2$, but increased to 202 km$^2$ when 23 LC-B locations were included. The

male's home range was underestimated due to a 4-month gap in locations (mid-Sep–mid-Jan) that occurred while it traveled from the capture area to an area beyond the western park boundary (Fig. 2).

The PTT-collared female was lost from both VHF and PTT contact for 3 months (Mar–May 2000). We suspected that this was related to her occupying a birthing den that blocked signal reception. In November 2000 we observed her, and although we did not see cubs, she made vocalizations that mothers use to call cubs.

The maximum distance across MCP home ranges averaged 18.1 km (SD = 6.7, range: 10.9–30.9 km, $n$ = 8); 2 of them were more than half the distance across the park (44 km). At least 4 bears, 3 adult and 1 subadult males (half the bears that we routinely tracked), moved outside the park boundaries (up to 6 km; Fig. 2). They remained outside the park for 2 months to >1 year. Two bears moved beyond the western boundary of the park and remained on national forest lands without road systems (Fig. 2). The other 2 moved outside the southeastern boundary in early spring; we subsequently lost track of 1 of these.

All radiotracked bears that occupied Daphan in fall left this oak-dominated area by December–January. Centers of fall ranges for 6 males in Daphan were separated from their ranges the following spring by 6.5–15.4 km ($\bar{x}$ = 11.3, SD = 5.8 km). These bears moved little from spring to summer: spring and summer ranges of each individual were centered only 2.3–2.9 km apart. Only 1 of these males returned to Daphan the following year.

The only female bear with sufficient data, mainly PTT locations, also returned to Daphan in 2 consecutive acorn seasons. Her collar fell off and was collected only 6 m from her capture site in the 2002 acorn season, 3 years after the collar was deployed. She had what appeared to be the largest summer (87 $km^2$) and fall ranges (52 $km^2$) among all radiotracked bears (male seasonal ranges were only 4–14 $km^2$). Her spring range appeared to be located within her fall range, although data were limited to February, before she apparently denned. Her seasonal ranges overlapped extensively and the centers were close, 1.3–2.1 km ($n$ = 3).

### *Elevational movements and habitat use*

Radiolocations of bears covered a wide elevational span, 300–2,790 m, with distinct seasonal changes. In spring, 72% of locations occurred at elevations of 500–1,500 m (Fig. 3; total range = 300–2,390 m). Summer locations tended to be at higher elevations, with 70% at 1,000–2,000 m (range 290–2,560 m). In fall, 92% of locations were in the 1,000–2,000 m elevational band (range 940–2,790 m).

These same elevational range shifts occurred for 6 individual bears tracked during all 3 seasons, indicating that this finding was not attributable to the somewhat varying sample of individuals that we tracked each season. Differences in elevation were detected among these individual bears ($F$ = 6.85; 5, 154 df; $P$ < 0.0001, two-way ANOVA) and among seasons ($F$ = 5.55; 2, 154 df; $P$ = 0.0047), but not for bear–season interaction ($F$ = 1.77; 10, 154 df; $P$ = 0.07), indicating that these individual bears exhibited similar seasonal shifts in elevation. Scheffe's test indicated a significant elevational difference between spring ($\bar{x}$ = 1,140, SD = 467, $n$ = 43) and summer ($\bar{x}$ = 1,370, SD = 490, $n$ = 84; $P$ = 0.032), and between spring and fall ($\bar{x}$ = 1,520, SD = 379, $n$ = 45; $P$ = 0.001), but not between summer and fall ($P$ = 0.23).

Overall, throughout the year, bears selected areas below 2,000 m elevation: 92.3% of radiolocations were below 2,000 m, whereas only 69.5% of the area circumscribed by MCP home ranges and only 42.5% of the study area was <2,000 m. Individual home ranges of bears varied, however. Four of 8 bears had 89–100% of their home range area <2,000 m, 2 had 55–72%, and 2 had only 20–38% of their home range below this elevation. One subadult male (MS6, Table 2) lived at a considerably higher elevation than the others, with nearly 50% of its range, although none of its actual radiolocations (1,200–2,400 m, $n$ = 10), above 2,500 m. MCP home ranges of 3 bears encompassed areas >3,000 m, but no bears were ever located at this high of an elevation. Bear home ranges included areas of 500–2,000 m (CSI > 0.2) somewhat more than expected given the area of elevational bands available within the study area (CSI expected = 0.125), and included high elevation (>3,000 m) subalpine and alpine areas significantly less than expected (expected CSI > 95% CI; Table 2).

Home ranges of bears were comprised primarily of broadleaved forests, coniferous forests, and mixed broadleaved–coniferous forests; these 3 habitat types each comprised, on average, >30% of home range area (Table 3). Bear use of habitats (i.e., radiolocations) closely matched availability of habitats within home ranges (Table 3). Home ranges included mixed broadleaved–coniferous forests more than expected

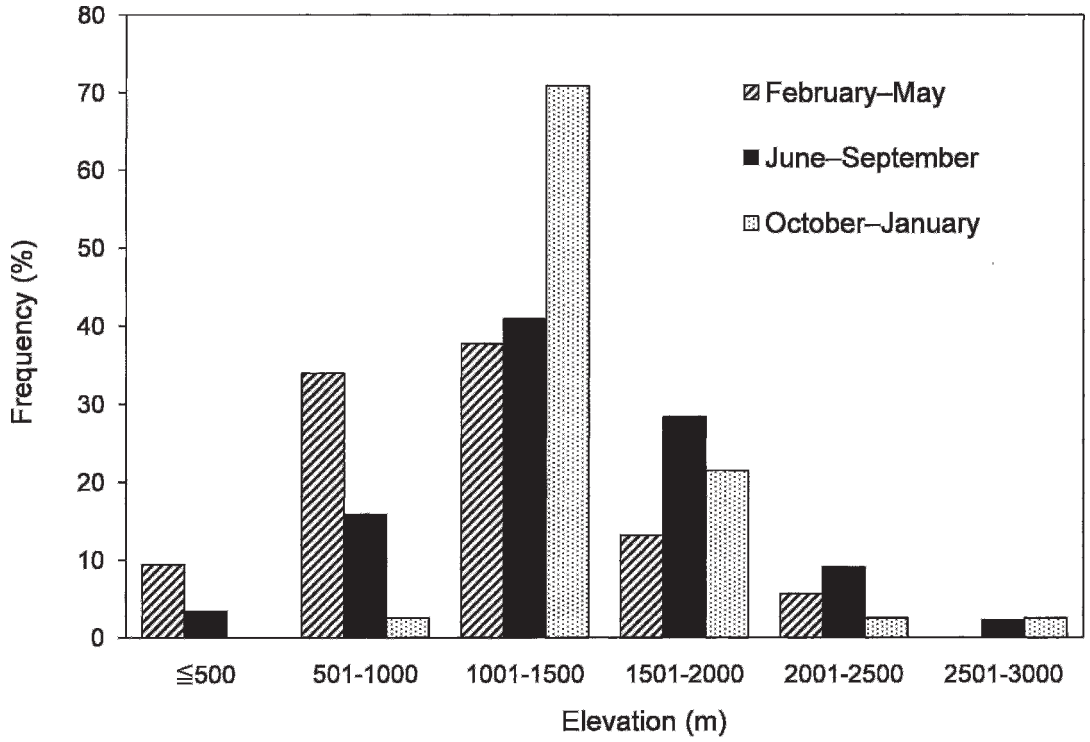


**Fig. 3. Seasonal differences in elevations of radiolocations ($n$ = 220) of Formosan black bears in Yushan National Park, Taiwan, 1998–2001.**

**Table 2. Comparison of elevational composition of the study area in Yushan National Park, Taiwan, to the distribution of radiolocations of Asiatic black bears and the composition of minimum convex polygon (100% MCP) home ranges defined by those radiolocations for data collected 1998–2001. Chesson selection indices (Chesson 1978, 1983) for second-order selection of 8 elevational bands are shown for 8 bears. A value of 0.125 indicated use of elevational zone in proportion to availability; 95% CI not including this value indicated use more or less than expected.**

| Elevational zone (m) | % Study area | % Radio locations | Mean (SD) of % individual MCP | | Chesson selection indices (CSI)[a] | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Bear ID[b] | | | | | | | | | | 95% CI | |
| | | | | | MA2 | MA4 | MS5 | MS6 | FA7 | MA8 | MA11 | MA13 | Mean | (SD) | SE | Lower | Upper |
| 0–500 | 1.7 | 3.6 | 2.3 | (3.7) | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.2 | 0.3 | 0.10 | (0.14) | 0.05 | −0.01 | 0.21 |
| 500–1000 | 5.9 | 15.5 | 15.3 | (19.2) | 0.2 | 0.2 | 0.4 | 0.0 | 0.1 | 0.0 | 0.4 | 0.5 | 0.22 | (0.20) | 0.07 | 0.05 | 0.39 |
| 1000–1500 | 13.3 | 50.5 | 24.0 | (13.2) | 0.4 | 0.5 | 0.2 | 0.0 | 0.3 | 0.1 | 0.2 | 0.1 | 0.23 | (0.13) | 0.05 | 0.11 | 0.34 |
| 1500–2000 | 21.6 | 22.7 | 27.9 | (11.9) | 0.3 | 0.3 | 0.1 | 0.2 | 0.3 | 0.3 | 0.1 | 0.0 | 0.20 | (0.11) | 0.04 | 0.11 | 0.29 |
| 2000–2500 | 25.0 | 5.9 | 19.1 | (14.2) | 0.1 | 0.1 | 0.0 | 0.3 | 0.2 | 0.3 | 0.0 | 0.0 | 0.14 | (0.12) | 0.04 | 0.03 | 0.24 |
| 2500–3000 | 23.0 | 1.8 | 10.0 | (14.2) | 0.0 | 0.0 | 0.0 | 0.3 | 0.1 | 0.2 | 0.0 | 0.0 | 0.09 | (0.12 ) | 0.04 | −0.02 | 0.19 |
| 3000–3500 | 8.8 | 0 | 1.4 | (3.0) | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.1 | 0.0 | 0.0 | 0.03 | (0.07) | 0.02 | −0.02 | 0.09[c] |
| 3500–4000 | 0.7 | 0 | 0 | (0) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 | (0.01) | 0.00 | −0.01 | 0.02[c] |

[a]Use = elevational composition of bear home range; availability = elevational composition within the study area. Values are rounded for clarity, causing some columns to appear to not to sum to 1.0.
[b]FA = female adult; MA = male adult; MS = male subadult.
[c]Significantly underused elevational zones: upper 95% CI < 0.125.

**Table 3. Comparison of vegetation composition of the study area in Yushan National Park, Taiwan, to the distribution of radiolocations of Asiatic black bears and the composition of minimum convex polygon (100% MCP) home ranges defined by those radiolocations. Chesson selection indices (Chesson 1978, 1983) for second-order selection of 8 vegetation types are shown for 8 bears. A value of 0.125 indicated use of vegetational type in proportion to availability; 95% CI not including this value indicated use more or less than expected.**

| Vegetation type | % Study area | % Radio locations | Mean (SD) of % individual MCP | Chesson selection indices (CSI)[a] | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Bear ID[b] | | | | | | | | | | 95% CI | |
| | | | | MA2 | MA4 | MS5 | MS6 | FA7 | MA8 | MA11 | MA13 | Mean (SD) | SE | Lower | Upper |
| Broadleaved forest | 24.3 | 31.7 | 31.9 (24.3) | 0.3 | 0.5 | 0.2 | 0.0 | 0.0 | 0.0 | 0.2 | 0.2 | 0.18 (0.15) | 0.05 | 0.06 | 0.31 |
| Mixed broadleaved –coniferous forest | 19.2 | 30.4 | 30.8 (11.7) | 0.4 | 0.3 | 0.2 | 0.1 | 0.2 | 0.2 | 0.3 | 0.1 | 0.24 (0.10) | 0.04 | 0.15[c] | 0.32 |
| Coniferous forest | 46.4 | 28.6 | 31.9 (26.8) | 0.0 | 0.0 | 0.0 | 0.3 | 0.2 | 0.2 | 0.0 | 0.0 | 0.10 (0.10) | 0.03 | 0.02 | 0.18 |
| Grassland | 2.5 | 1.3 | 0.3 (0.3) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.02 (0.02) | 0.01 | 0.00 | 0.03[c] |
| Bamboo shrubland | 3.0 | 0 | 1.0 (2.0) | 0.0 | 0.0 | 0.0 | 0.3 | 0.1 | 0.1 | 0.0 | 0.0 | 0.05 (0.11) | 0.04 | −0.04 | 0.15 |
| Open area | 3.1 | 4.0 | 2.9 (1.6) | 0.0 | 0.1 | 0.1 | 0.2 | 0.2 | 0.1 | 0.1 | 0.2 | 0.13 (0.06) | 0.02 | 0.08 | 0.17 |
| Riparian | 0.5 | 4.0 | 1.2 (0.8) | 0.2 | 0.1 | 0.4 | 0.1 | 0.3 | 0.3 | 0.4 | 0.5 | 0.28 (0.13) | 0.05 | 0.16[c] | 0.39 |
| Agricultural land | 0.9 | 0 | 0.0 (0.0) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 (0.00) | 0.00 | −0.01 | 0.01[c] |

[a]Use = vegetational composition of bear home range; availability = vegetational composition within the study area. Values are rounded for clarity, causing some columns to appear to not to sum to 1.0.
[b]FA = female adult; MA = male adult; MS = male subadult.
[c]Use significantly more than expected if lower 95% CI value >0.125, and less than expected if upper CI < 0.125.

(expected CSI [0.125] < 95% CI) based on availability of this habitat in the study area (second-order selection; Table 3). Home ranges also included more broadleaved forests than expected, but not significantly so. Home ranges included significantly more riparian habitat than expected, but this habitat comprised only 0.5% of the study area and home ranges contained only twice that, which may be biologically insignificant. Bears were located in grassland meadows only 1.3% of the time, and were never located in agricultural lands or bamboo shrub lands.

### *Movements and social interactions related to acorn production*

Movements of bears in fall were related to the availability of acorns, which fluctuated by oak species and by year. In 1998, acorn production of ring-cupped oaks in Daphan was abundant over an area >12 km$^2$. In 1999, acorn production by ring-cupped oaks was poor, although Arishan oak (*Quercus stenophylloides*) was productive; this species is scattered less densely surrounding the highly-concentrated ring-cupped oak forest at Daphan. In 2000, the acorn crop in Daphan was good, but concentrated in a small (2 km$^2$) patch, while other hard mast foods for bears in surrounding areas were sparse due to severe typhoon damage in late August.

Capture rates, amount of bear sign, and telemetry data indicated that during good acorn-production years (1998, 2000), more bears congregated and stayed longer in Daphan than during an acorn failure (1999; Table 4). In fall 1998, all 4 adult bears that had been caught and collared at Daphan consistently used a small portion of this area (<1 km$^2$) for about 7 weeks (Table 4). They all left Daphan when availability of acorns declined by early January. In fall 1999, only 1 of 6 radiocollared bears came back to Daphan; that bear immediately left for an area about 2 km south, where Arishan oak was experiencing high mast, and stayed there during October–December. We could not relate bear use of Daphan to acorn abundance in 2001 because construction of a bridge on a nearby foot trail (including many workers, noisy machines, and loads of materials dropped by helicopter) apparently deterred bears from the area; fresh feeding sign appeared in January 2002, immediately after the construction was completed.

Bear use of Daphan in fall varied by sex and age. In 1998 and 2000, when ring-cupped oak acorns were readily available, we captured 9 adult males and only 1 female from late October to mid-November. The other female was caught at Daphan in 1999, when there were few other bears. This female was observed in Daphan again in early

**Table 4. Relationship between acorn production, which varied among years, and indices of Asiatic black bear abundance and activity in an oak-rich area (Daphan) of Yushan National Park, Taiwan, 1998–2000.**

| Parameter | 1998 | 1999 | 2000 |
|---|---|---|---|
| Relative acorn production[a] | Very good, extensive | Poor | Good, but concentrated |
| Number of bears captured[b] | 6 (5M, 1F) | 1 (F) | 7 (7M) |
| Trap-nights/capture | 116 | 967 | 57 |
| Number of scats collected | 263 | 1 | 295 |
| Date of first capture (mm/dd/yyyy) | 10/25/1998 | 12/09/1999 | 11/06/2000 |
| Date of last signal reception (mm/dd/yyyy) | 01/05/1999 | Rarely heard | 12/04/2000 |
| Duration of occupancy by bears (weeks)[c] | 7 | <1 | 2 |

[a]Subjective rating.
[b]F = female; M = male.
[c]Time from the first bear sign (scats or foraging signs) to last reception of a radio signal in the area.

November 2000. However, a few days later we had indications of an influx of adult males, of which we caught 6 in 8 days. The female quickly vacated the area where she had been feeding (the most productive spot) and moved away from Daphan to a higher elevation (>1,500 m) where ring-cupped oaks were much less abundant.

Of the 12 males captured at Daphan, only 3 were subadults. One of these was caught during the peak of the acorn season but immediately left the area, whereas the other 2 were caught late in the season when most of the larger bears in the area had left. In 2000, when the foraging area was most restricted, we heard agonistic vocalizations by bears several times, which were never heard in 1998 or 1999.

## Discussion

We posed 2 hypotheses, 1 that was supported by our findings and 1 that was not. We found that bears used a variety of elevations commensurate with changing food availability (hypothesis 1). However, these elevational movements apparently were not sufficient to satisfy all the bears' needs, as they also moved laterally, sometimes large distances, across the landscape. Contrary to our second hypothesis, this park was not large enough to contain these bears.

### *Home range size and estimation*

Our study indicated that individual bears used a large proportion of the area of YNP and also often spent time outside the park. Our actual data certainly underestimated both the size of the home ranges and use of areas outside the park. Most reliable radiolocations that we obtained were within 3 km of trails or roads, and there were very few trails and roads along the park boundary. In several cases, we could detect radio signals from a distant bear, but could not obtain acceptable triangulated radio-bearings to attain a location. Aerial telemetry and PTT collars provided locations of bears in inaccessible areas, greatly increasing home range estimates in some cases. Even the PTT collars, however, did not produce locations (or locations with acceptable accuracy) in all areas, apparently due to the signal being blocked by rugged terrain or dense vegetation. The perceived range of an adult female (FA7) with a PTT collar would have been 15% smaller had a single aerial location not been obtained (Fig. 2). However, aerial telemetry was constrained by expense ($1,500–$2,400/hour, 1999) and safety concerns (related to unpredictable weather).

Studies of other wide-ranging species reported that home range sizes derived from satellite (GPS or PTT) transmitter data were about 2.5x larger than those derived from VHF data (Ballard et al. 1998, Arthur and Schwartz 1999). Satellite-acquired data yield larger home ranges because of the greater number of locations, acquisition of locations in areas or at times unavailable using VHF telemetry, and also possibly more errors associated with PTT locations. PTT errors may arise from various sources (Keating 1995, Mate et al. 1997) and tend to be most problematic in circumstances like that in YNP, with mountainous terrain and dense canopy, which can block signal reception. However, our low-accuracy locations (LC-B or A) were clustered together with the few high-accuracy locations, as has been reported in other studies (Stüewe et al. 1998). The clusters of PTT locations also generally coincided with places where VHF signals were detected aerially or from the ground, suggesting that errors for the PTT points that we used did not significantly affect our estimates of home range size. Other studies have indicated that PTT errors are not large enough to

account for the differences between estimates of home range sizes derived from PTT and VHF datasets for highly mobile animals, like bears (Ballard et al. 1998, Schwartz and Arthur 1999).

Our home range estimates for bears based only on ground tracking (24–71 $km^2$) were within the range of estimates obtained previously in temperate environments. Minimum annual home ranges for 2 male Asiatic black bears in southwestern China were 16 and 37 $km^2$ (Reid et al. 1991). In Japan, Ohsako (1995) reported home ranges of 33 $km^2$ for a male and 20 $km^2$ for a female, and Izumiyama and Shiraishi (2004) reported multi-annual ranges (2–4 years) of 45–123 $km^2$ for males ($n$ = 3) and 33–96 $km^2$ for females ($n$ = 4). Asiatic black bears in these areas exhibited similar diets to those in our study area (Hwang et al. 2002) and lived in similar mountainous, broadleaved forests. In the Russian Far East, where topographic relief is less, some Asiatic black bears ranged much farther (males: 31–1,090 $km^2$ [>2,000 $km^2$ for 1 bear including a seasonal migration during a poor mast year], median = 132 $km^2$, $n$ = 11; females: 16–25 $km^2$, median = 20 $km^2$, $n$ = 3; Kostyria et al. 2002). Only the Russian study employed aerial telemetry. The other studies were performed using ground telemetry, and as in our study, gaps in the data occurred when bears moved to inaccessible areas.

If researchers are able to locate radiocollared animals only when they are close enough to a limited number of roads and trails to hear the signal, home range sizes are likely to be substantially underestimated. In some studies, the access roads themselves may even appear to be centers of animal activity, while really only being centers of human observation (e.g., sun bears, *Helarctos malayanus*: Nomura et al. 2004, Wong et al. 2004). Reviews of telemetry and home range techniques have neglected this issue of sampling bias related to limited observer access (Harris et al. 1990, White and Garrott 1990, Kernohan et al. 2001).

In nearly all studies of ursid home ranges, males were found to use significantly (2–5x) larger areas than females (Garshelis 2009). That the largest annual home range in our study (117 $km^2$) was for a female is noteworthy—now being the largest female range reported for this species. The point is not that YNP bears have especially large home ranges, but that home range estimates derived from satellite collars (e.g., the female in our study) are likely closer to true home range size, and often much larger than gleaned from ground telemetry. Although variation among home range sizes appears to be larger for American than for Asiatic black bears (Garshelis 2004), we found only 3 of 41 studies of American black bears that reported average female home range sizes larger than the PTT-equipped bear in our study (Aune 1994, Pacas and Paquet 1994, Mosnier et al. 2008). This finding suggests that male home range sizes in our study were appreciably underestimated, and that the home range of 202 $km^2$, calculated for the 1 male with a PTT collar including LC-B locations, may be much closer to reality than our ground-based home range estimates.

### *Relationship of movements to food abundance*

The reason for the unexpectedly large home ranges in YNP likely has to do with the nature and distribution of food resources. Some bears shifted areas of use seasonally, especially between summer and fall, which expanded the size of their annual home ranges. Others, such as the PTT-collared female, had large seasonal ranges, each in the same vicinity. Within the scope of our study, we were unable to determine why bears had to travel across so many watersheds, each with a large span of elevational relief, to satisfy their living requirements. Their use of low elevations in spring corresponded with the availability of succulent green vegetation, and their movement to higher elevations in summer was related to availability of berries in the Lauraceae family, especially *Machilus* spp. (Hwang et al. 2002), as well as birthing of some potential mammalian prey (e.g., sambar deer, *Rusa unicolor*). In fall, bears were attracted to oak forest habitats. This pattern is similar to what has been reported in Japan, although unlike Japan (Huygens et al. 2003, Izumiyama and Shiraishi 2004), bears in our study rarely used subalpine and alpine areas (elevations >3,000 m).

Hard mast, especially acorns, is an important and preferred fall food for both Asiatic and American black bears (Mattson 1998, Vaughan 2002, Costello et al. 2003, Hashimoto et al. 2003). Acorns were found in 92–97% of fall scats during our study (Hwang et al. 2002). When ring-cupped oaks were productive, many bears congregated in Daphan and stayed there >2 months. When these acorns were scarce, bears were either more scattered among the few stands with available acorns, or did not use oak forests (which, aside from acorns, were depauperate of food). This general pattern of movement related

to varying abundance of acorns and other hard mast has been reported elsewhere (Japan: Hazumi and Maruyama 1986 and 1987, Huygens and Hayashi 2001, Oka et al. 2004; China: Reid et al. 1991; Russia: Khramtsov 1997, Kostyria et al. 2002).

In response to acorn failures, American black bears have been observed to greatly expand their fall ranges, often taking them outside the reserves that protect them (Pelton 1989, Powell et al. 1997, Kasbohm et al. 1998, Vaughan 2002). We could not assess whether this was also the case in YNP. We lacked adequate data to quantify fall home ranges when acorn abundance in Daphan was low because the bears were scattered over a wide area and often out of range of our ground telemetry. We observed, though, that when acorn production was poor, bears were more diurnal in their feeding and fed more on small ungulates (Hwang et al. 2002, Hwang and Garshelis 2007). Because local hunters (illegally hunting, often near the park periphery) attempted to trap these ungulates (Hwang 2003), it stands to reason that bears would be more attracted to hunters' traps in such years.

In a year of short-term acorn abundance (2000), bear density in Daphan appeared to be especially high but ephemeral as food supplies rapidly became depleted. Moreover, vocalizations indicated higher than normal levels of aggression between bears. We expect that in years when acorns are scarce, many bears travel widely. In our study, 1 bear captured close to Daphan during fall 2000 appeared to live mainly near the western border of the park the rest of the year (MA8, Fig. 2). Bears seemed to have a clear preference for ring-cupped oak acorns over other species of acorns, and the density of ring-cupped oak was higher in Daphan than in any other area in or near the park (that we were aware of). Thus, the highly localized nature of this resource may attract bears from distant areas.

Even in good acorn years, females and subadult males appeared to be excluded from Daphan. Either they did not come into the prime feeding area, or they fed there at different times (Hwang and Garshelis 2007). Exclusion of (or avoidance by) females and smaller males from prime feeding areas occupied by larger adult males is common among ursids (Asiatic black bear: Huygens and Hayashi 2001; American black bear: Garshelis and Pelton 1981, Chi 1999, Garneau et al. 2008; brown bear: Wielgus and Bunnell 1994, Ben-David et al. 2004; sloth bear [*Melursus ursinus*]: Joshi et al. 1999; polar bear: Stirling and Derocher 1990). The ramifications of this in YNP are unknown, but we speculate that it causes some bears, especially females, to move to areas near the edges of the park, where they are at greater risk from illegal hunters.

## Conservation implications

As bears and other wide-ranging animals become increasingly confined to isolated protected areas, especially in the tropics, it is imperative to ensure that these areas are sufficiently large or connected to other areas (or both) to enable the animals to travel with minimal risk of human contact (Clark and Pelton 1999, Jachmann 2008, Valenzuela-Galván et al. 2008). The sizes of home ranges we observed indicates that YNP, the largest park in Taiwan, is not large enough to contain and protect endangered Formosan black bears. The length of the observed home ranges indicates that almost any bear living in the most remote, central parts of the park could easily travel outside the park, and at least half the bears that we observed did so. We cannot generalize this finding to reserves of similar size outside Taiwan, given our limited understanding of what drives bears to use the large areas that they did. We know that food resources for bears in YNP were diverse (Hwang et al. 2002), but we lacked information on patchiness and covariation in fruiting that could have prompted bears to travel widely. Nevertheless, other ground-based telemetry studies of this species yielded similar range sizes to our ground-based estimates and encountered similar problems in tracking success, suggesting that they too would have underestimated the efficacy of reserves in protecting bears.

Bears that traveled near or beyond the boundary of the park almost certainly experienced greater risk from hunters. Our field observations and interviews with indigenous people in villages adjacent to the park indicated that hunting pressure within the core of the park was negligible, whereas hunting activity was high along the park's periphery (Hwang 2003). Most hunting was for ungulates, but bears were sometimes incidentally captured in snares and then killed. The fact that in our sample of 15 bears, 8 had missing toes or paws indicates that a large proportion of bears have had experiences in hunters' traps.

The irony highlighted in this study is that in rugged terrain with limited human access (Fig. 1) — ideal circumstances for protecting wildlife — com-

monly used research techniques such as ground telemetry may be inadequate to assess the true scale of animal movements. Hence, researchers relying on such data could gain a biased view of the adequacy of reserve size. We did find some wide-ranging bears near the park boundaries with ground telemetry. However, had it not been for our limited satellite and aerial telemetry data, we would have had a markedly different perception of how large an area YNP bears used (Fig. 2). Unfortunately, high-end technology comes with high costs, not only in terms of money but also in reliability: only 2 of 5 GPS-PTT units that we deployed provided data. Such equipment and techniques may be hard to justify to funders, but often may be needed to obtain accurate information of the effectiveness of reserves.

Given the absence of demographic data, we cannot comment on whether bears in YNP are adequately protected. As a flagship species for the Central Mountain Range, the only remaining sanctuary frontier for various large mammals of Taiwan, it is imperative that they are. We believe it is impractical to try to contain the bears within the park through habitat manipulations. The present habitat is diverse and mature; most (>75%) is undisturbed native vegetation, and the rest has recovered from human exploitation >40 years in the past. Modifications to this natural system would be unwarranted at this time, given our limited understanding of bears' resource needs. It is also not practical to recommend expanding the park boundaries, but given the continuous natural habitat surrounding the park, we suggest that establishing buffer zones around the park where human access would be more tightly controlled would be feasible and beneficial to bears. Results of this study also suggest that more patrolling along the edges of the park, possibly combined with community outreach with local villagers, may help protect wide-ranging female bears during the fall and winter, when local hunting is most prevalent and bears most apt to travel.

## Acknowledgments

We thank the Yushan National Park headquarters for providing research funding, equipment, logistical support, and helpful comments during the study. Additional funding for this research was provided by the John Sheldon Bevins Memorial Foundation, now called the Bear Conservation Fund, administered by the International Association for Bear Research and Management. Support at the University of Minnesota was provided by the MacArthur Program on Peace, Justice and Sustainability; the Conservation Biology Program; the James W. Wilkie Natural History Fund; and the Graduate School. We are grateful to the many volunteers who helped with fieldwork. We thank D. Reid and an anonymous reviewer for comments that helped improve the manuscript.

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*Received: 9 September 2009*
*Accepted: 5 December 2009*
*Associate Editor: S. Ratnayeke*