Home Ranges and Habitat Use of Sloth Bears *Melursus Ursinus Inornatus* in Wasgomuwa National Park, Sri Lanka

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We studied home ranges and habitat selection of 10 adult sloth bears *Melursus ursinus inornatus* at Wasgomuwa National Park, Sri Lanka during 2002-2003. Very little is known about the ecology and behaviour of *M. u. inornatus*, which is a subspecies found in Sri Lanka. Our study was undertaken to assess space and habitat requirements typical of a viable population of *M. u. inornatus* to facilitate future conservation efforts. We captured and radio-collared 10 adult sloth bears and used the telemetry data to assess home-range size and habitat use. Mean 95% fixed kernel home ranges were 2.2 km^2 (SE = 0.61) and 3.8 km^2 (SE = 1.01) for adult females and males, respectively. Although areas outside the national park were accessible to bears, home ranges were almost exclusively situated within the national park boundaries. Within the home ranges, high forests were used more and abandoned agricultural fields (chenas) were used less than expected based on availability. Our estimates of home-range size are among the smallest reported for any species of bear. Thus, despite its relatively small size, Wasgomuwa National Park may support a sizeable population of sloth bears. The restriction of human activity within protected areas may be necessary for long-term viability of sloth bear populations in Sri Lanka as is maintenance of forest or scrub cover in areas with existing sloth bear populations and along potential travel corridors.

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The sloth bear *Melursus ursinus* is a myrmecophagous (ant- or termite-eating) ursid found in India, Nepal, Bhutan, Bangladesh and Sri Lanka. The sloth bear is listed as 'vulnerable' by the World Con-

servation Union (IUCN 2004); the species' range has become increasingly fragmented and many sloth bear populations outside protected areas are believed to be decreasing or to have disappeared entirely (Krishnan 1972, Santiapillai & Santiapillai 1990, Servheen 1990, Garshelis et al. 1999b).

M. u. inornatus, one of two recognized subspecies of the sloth bear, is about ⅔ of the size of bears on the Indian mainland and tends to have shorter hair. It is possibly Sri Lanka's most vulnerable carnivore (Santiapillai & Santiapillai 1990). Human densities are high in Sri Lanka and both protected and unprotected areas experience poaching and human encroachment. Behavioural and life history characteristics of sloth bears place them at risk throughout most of their range (Garshelis et al. 1999b). In many portions of their range, sloth bears are rare where human disturbance is high. When disturbed, sloth bears may respond aggressively and attack and injure humans (Santiapillai & Santiapillai 1990, Rajpurohit & Krausman 2000), often resulting in their persecution (S. Ratnayeke, unpubl. data). Sloth bears have one of the lowest reproductive rates among carnivores (Gittleman 1989) and, by virtue of their size, may require large areas of relatively undisturbed habitat to maintain viable populations. Apart from a few studies in Nepal (Joshi et al. 1995) and India (Akhtar et al. 2004; K. Yoganand, pers. comm.), very little is known about the use of space or habitats by the sloth bear (Garshelis et al. 1999b).

Myrmecophagous mammals tend to have small home ranges relative to their body size (McNab 1983, Shaw et al. 1985, 1987). Conversely, large Carnivora, such as ursids, have large home ranges (McLoughlin et al. 1999, Garshelis 2004) and may demonstrate marked shifts in the location of their home ranges in response to seasonal changes in resources (Garshelis & Pelton 1981, Blanchard & Knight 1991, Dahle & Swenson 2003). Home ranges can therefore provide valuable information for conservation because they reflect the metabolic needs and the distribution and abundance of resources, such as food and mates, in a population (McNab 1963, Harvey & Clutton-Brock 1981, Gittleman & Harvey 1982, McDonald 1983).

Within their geographical range, sloth bears use a wide range of habitats (e.g. grasslands, scrub and forests in dry or wet regions; Garshelis et al. 1999b). In Sri Lanka, however, sloth bears are confined to the relatively remote areas of the dry zone lowlands (Phillips 1984). In the absence of any empirical data on the ecology of *M. u. inornatus*, our purpose was to determine home-range sizes and habitat use of sloth bears as a first step towards designing conservation initiatives for this subspecies. We defined habitat as a set of environmental components (Garshelis 2000, Morrison 2001), namely vegetation types or human disturbance, within a defined area. We then tested whether sloth bears selected particular habitat types to establish home ranges and if certain habitat types within home ranges were used more or less than expected.

Material and methods

Study area

Our study site was located in Wasgomuwa National Park (39,385 ha) in the central region (80°55'E, 7°45'N) of Sri Lanka (Fig. 1). The national park is in the lowlands of Sri Lanka where the climate is classified as Tropical Dry Zone (Domrös 1974). With respect to rainfall, the area is at the transition of the intermediate and dry climatic zones of the island. Most of the mean annual precipitation of 1,800 mm occurs from November through January (Pabla et al. 1998). Elevation ranges within 60-200 m a.s.l. with undulating terrain intercepted by a long ridge (300-1,000 m) extending north-south. Temperatures are uniformly high throughout the year, with an annual mean of 32°C. The predominant soil type of the national park is shallow to moderately deep reddish brown earths in low relief areas, narrow extents of alluvial soils adjoining rivers and streams, and a complex of shallow gravelly reddish brown earths and regosols on steeper mountain ridges (Pabla et al. 1998).

The national park has a high diversity of flora and fauna, including large herbivores, such as elephants *Elephas maximus*, buffalo *Bubalus bubalis*, sambar *Cervus unicolor*, and spotted deer *Axis axis*. Apart from sloth bears, 13 other species of Carnivora occur in Wasgomuwa National Park, including the leopard *Panthera pardus* (S. Ratnayeke, unpubl. data). The vegetation of Wasgomuwa National Park is broadly classified as dry monsoonal forest, which typically consists of a mosaic of vegetation types differing in structure and composition (Jayasingham et al. 1992).

The national park is bound by rivers on the north, east and west boundaries. On the northern boundary, the park is linked to other protected areas to facilitate movements of elephants. Agricul-
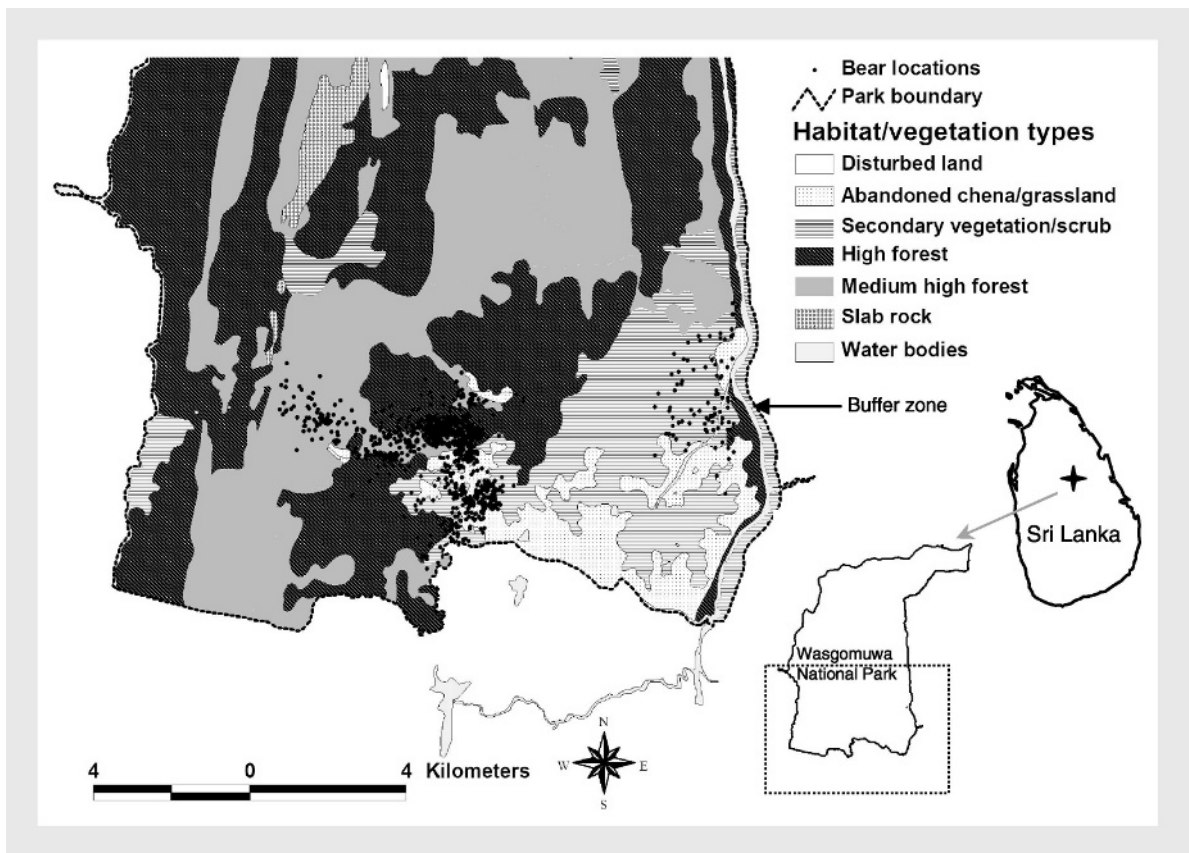
Figure 1. Location of Wasgomuwa National Park, Sri Lanka, and the region of the park used to determine home ranges and habitat use of sloth bears during 2002-2003. Original habitat cover classes were derived from Pabla et al. (1998). Habitat types that occurred in very small proportions within home ranges were consolidated with habitat types of similar structural attributes or community composition. The buffer zone was a belt of forest on the east bank of the river, which is the eastern boundary.

ture, village gardens and settlements occur on the southern boundary of the national park. The eastern boundary has a 300-500 m buffer zone of forest, along which are agricultural fields and scattered settlements. Villagers routinely use the river banks on the east and southwest boundaries for bathing, fishing, herding cattle and gathering firewood. Except during months when monsoon rains are heavy (November-January), the rivers on both the east and west boundaries are easily crossed by humans and animals, although they retain some water throughout the dry season. Legal entry into national parks requires permits, and visitors are allowed to traverse the park only during daytime in a vehicle accompanied by a Department of Wildlife Conservation (DWLC) guide.

Capture and telemetry

We captured sloth bears in barrel traps in 2002 and 2003. The Sri Lanka DWLC permitted the capture and radio-collaring of a maximum of 10 adult bears. The animal handling protocol was reviewed and approved by DWLC veterinarians, and a regional DWLC veterinarian attended every capture to assist with immobilization and handling. Traps were baited with honey from wild bees. Upon capture, bears were immobilized with an intramuscular injection of ketamine hydrochloride (4 mg/kg body mass) and xylazine hydrochloride (2 mg/kg; Joshi et al. 1995). We deployed radio-transmitters (MOD-500, Telonics Inc., Mesa, Arizona, USA) on 10 bears; radio-transmitters were designed to fall off within two years by use of a spacer (Hellgren et al. 1988) consisting of untreated leather.

Bears were located by triangulation from a vehicle or on foot using a receiver and a hand-held H-antenna (Telonics, Inc., Mesa, Arizona, USA). We used a global positioning system (GPS) receiver (Garmin Etrex, Olathe, Kansas, USA) to determine coordinates of stations from where azimuths were taken or to determine positions of visual observations of bears. In some instances, bears sensed our

presence when we located them by foot and would leave the site before being seen. We only documented the position of those bears if we could locate their rest site. We used two azimuths to estimate locations by triangulation using program Telem88 (Coleman & Jones 1988). We collected 4-6 locations per animal per week. Tracking schedules for each bear were distributed throughout the 24-hour period. All radio transmitters were equipped with a mercury tip switch, which allowed us to determine whether bears were active or resting by monitoring changes in the pulse rate of the radio signal. Changes in pulse mode usually followed a change in head/body position, whereas changes in signal strength usually were associated with locational movements. Although neither of these changes alone were precise appraisals of activity, we used the combination of the two methods to assess whether bears were active or resting. Janis et al. (1999) found that ≥ 3 pulse mode changes per minute correctly classified mountain lions *Puma concolor* as active 57-94% of the time. We recorded a bear as active if we heard ≥ 3 changes in pulse mode or signal strength per minute during a 3-minute period.

We determined telemetry error by placing test transmitters in areas used by sampled bears and from positions typically used to obtain radio locations. For these tests, field personnel did not know the location of the transmitters. We used the distances between the triangulated locations and the GPS locations of the test collars to generate a distribution of error distances (N = 59).

Home ranges

Most radio-locations used for home-range delineation were obtained ≥ 24 hours apart (median = 26.7 hours, $\bar{x}$ = 92.8). We delineated 95% fixed kernel home ranges for each bear (Worton 1987, 1989). Seaman et al. (1999) recommended a minimum of 30-50 locations for this technique. For bears with > 55 locations, home ranges based on the first 40 locations ($\bar{x}$ = 2.00 km^2, SE = 0.25) were not different (Wilcoxon test: N = 6, P = 0.4) from those based on all locations ($\bar{x}$ = 2.15 km^2, SE = 0.38). Therefore, we used 40 locations as our minimum. Like most home-range estimators, kernel home ranges represent intensity of use of certain areas and are based on the assumption that topography, vegetation features or movements do not hamper the location of individuals. We could almost always locate all bears during telemetry sessions so calculating utility distributions was appropriate. We also

determined minimum convex polygon (100% MCP) home ranges (Mohr 1947) for comparison with other studies and for bears with < 40 seasonal locations. All home ranges were calculated using the Animal Movement extension (Hooge & Eichenlaub 1997) to ArcView® geographic information system (GIS; ESRI, Redlands, California, USA).

We compared seasonal shifts in home ranges by calculating the distance between arithmetic centers of activity of bear locations during wet and dry seasons (Joshi et al. 1995). We defined the wet season as mid-October to mid-May. Although most precipitation occurred from November through January, intermonsoonal precipitation resulted in some water retention in streams and waterholes, and soils remained relatively moist through April. The dry season extended from mid-May to mid-October, which was typical of the region (Domrös 1974). We used Mann-Whitney U-tests to compare home-range sizes of males and females, and we used Wilcoxon signed-ranks tests (Sokal & Rohlf 1995) to compare differences in size among paired sets of seasonal ranges for each bear.

Habitat use analysis

All telemetry locations of sloth bears were incorporated into a GIS for overlay with digital maps of habitat types obtained from the Department of Wildlife Conservation (DWLC; Pabla et al. 1998). The maps were digitized by the DWLC from 1:50,000-scale land use maps (1991 data, Sri Lanka Survey Department, Colombo, Sri Lanka), and land use was extracted based on aerial photographs. Compiled information was field-validated (Perera & Shantha 1996). Aerial photographs combined with ground truth data were used to update the maps in 1997 (DWLC, unpubl. data). Habitat has not changed substantially since 1997. Although the southeastern portion of the protected area experienced encroachment in the 1960s, the area was declared a national park in 1984 and human activity in encroached areas was terminated.

Although eight habitat types occurred within the study area (Pabla et al. 1998), only six types occurred within sloth bear home ranges. The relative proportion of one habitat type within home ranges (forest on levees) was small (< 1%). Small areas of forests on levees were grouped with high forest based on their shared attributes of closed canopy structure and tree height (Table 1). We combined very small areas (< 1 ha) of slab rock, water holes and streambeds with the vegetation types in which

Table 1. Description of habitat classes to determine habitat use of sloth bears in Wasgomuwa, Sri Lanka, during 2002-2003, and proportion of each habitat type within the composite home range (2385.3 ha). Tree and shrub species included in the description of habitat classes represent dominant species.

Habitat class	Description	Original vegetation map classes in study area	Proportion
Abandoned chena	Grassland consisting of short grasses with scattered trees (*Diospyros ferrea, Manilkara hexandra*) and scrub (*Carissa spinarum, Flueggia leucopyrus*)	Abandoned chena	0.14
Secondary vegetation	Scrub (*Carissa spinarum*), or low stature forest (*Diplodiscus verucosus, Drypetes sepiaria*). Large canopy openings.	Secondary vegetation/scrub	0.35
High forest	Tall forest (*Diospyros ebenum, Drypetes sepiaria*) on slopes and undulating plain. Closed canopy.	High forest Forest on levee	0.24
Medium-high forest	Medium-high forest (*Drypetes sepiaria, Pterospermum canescens*) on low slopes and undulating plain. Open canopy degraded forest.	Medium-high forest	0.23
Disturbed land	Land outside national park boundaries. Dominant vegetation is similar to abandoned chena and secondary vegetation	Vegetation outside national park (includes abandoned chenas, secondary vegetation and agricultural fields	0.04

they occurred. Finally, we classified the eastern river bed, the national park buffer zone, and areas outside park boundaries as disturbed land. Disturbed land, which consisted mostly of used and abandoned agricultural fields (chenas), scattered homesteads and patches of scrub and grassland, differed from all other habitat types in that human access was unregulated (see Fig. 1).

We used an index of selectivity (Chesson index; Chesson 1978, 1983) to determine whether sloth bears used the five habitat types we defined in proportion to their availability within the home range (third-order habitat selection; Johnson 1980). We used the individual, rather than the radio-location, as the sample unit. We used ArcView® GIS to cal-

culate habitat associations of radio-locations and to determine the area of habitat polygons within each home range. For each bear, we calculated the Chesson index for each of the five habitat types according to:

$$\alpha_i = \frac{U_i/A_i}{U_i/A_i + U_j/A_j + U_k/A_k + U_l/A_l + U_m/A_m}$$

where U_i is the proportion of bear radio-locations within habitat type i, U_{j-m} are the proportions of radio-locations in the other four habitat types and A_{i-m} are the available proportions of the five habitat types within the kernel home range. An index value

Table 2. Capture data and estimates of home-range areas of sloth bears in Wasgomuwa National Park, Sri Lanka, during 2002–2003.

Bear ID	Mass at capture (kg)	Month of first capture (mo/yr)	Monitored up to (mo/yr)	No of locations obtained	No of months tracked	Home-range area (km²)	
						95% fixed kernel	Minimum convex polygon
Males							
# 030	80	06/2003	12/2003	40	7	8.06	5.07
# 970	85	06/2003	12/2003	48	7	5.47	3.50
# 700	65	06/2002	04/2003	56	10	2.84	3.18
# 350	70	06/2002	07/2003	76	14	2.57	4.19
# 270	76	07/2003	12/2003	49	6	2.03	1.83
# 941	73	06/2002	12/2003	104	18	1.71	4.70
Mean	75					3.78	3.75
Females							
# 310	67	06/2003	12/2003	49	7	3.93	3.29
# 200	58	07/2002	04/2003	102	14	2.06	2.50
# 450	54	06/2002	12/2003	139	18	1.60	2.45
# 250	51	06/2002	12/2003	151	18	1.18	1.59
Mean	58					2.19	2. 46

Table 3. Number of locations per time period and percentage of locations recorded as active of sloth bears in Wasgomuwa National Park, Sri Lanka, during 2002-2003.

Time period	No of locations	Percent active
17:00-19:00	105	57.7
20:00-22:00	97	61.7
23:00-01:00	56	57.5
02:00-04:00	49	57.3
05:00-07:00	86	54.4
08:00-10:00	141	31.2
11:00-13:00	132	24.7
14:00-16:00	148	26.5

of 0 would indicate that the habitat type was not used at all. Conversely, a value of 1.0 only occurs if the analyzed habitat type was used exclusively. Because we analyzed five habitat types, a Chesson index of 0.20 would indicate no selection for a habitat type. Indices > 0.20 and < 0.20 would indicate greater and lesser use, respectively, than expected. To determine whether selection occurred, we first calculated the standard error and 95% confidence interval of the Chesson index for each habitat type for the radio-collared bears. We considered selection significant if the 95% confidence interval did not include 0.20. Zero proportions of habitat use or availability were replaced with a value of 0.001. We used ArcView® GIS to calculate habitat associations of radio-locations and to estimate areas of habitat polygons within home ranges.

We assessed whether telemetry error affected the outcome of the habitat analysis by repeating the habitat use analysis with locations that incorporated error distances. Using the original locations as starting points, we created new locations at distances randomly chosen from the distribution of telemetry error distances and using a random azimuth. We then used the habitat associations of those new locations (error locations) to repeat the analysis as recommended by Nams (1989). Because error distances were randomly derived from a larger distribution of distances, we repeated this analysis 10 times.
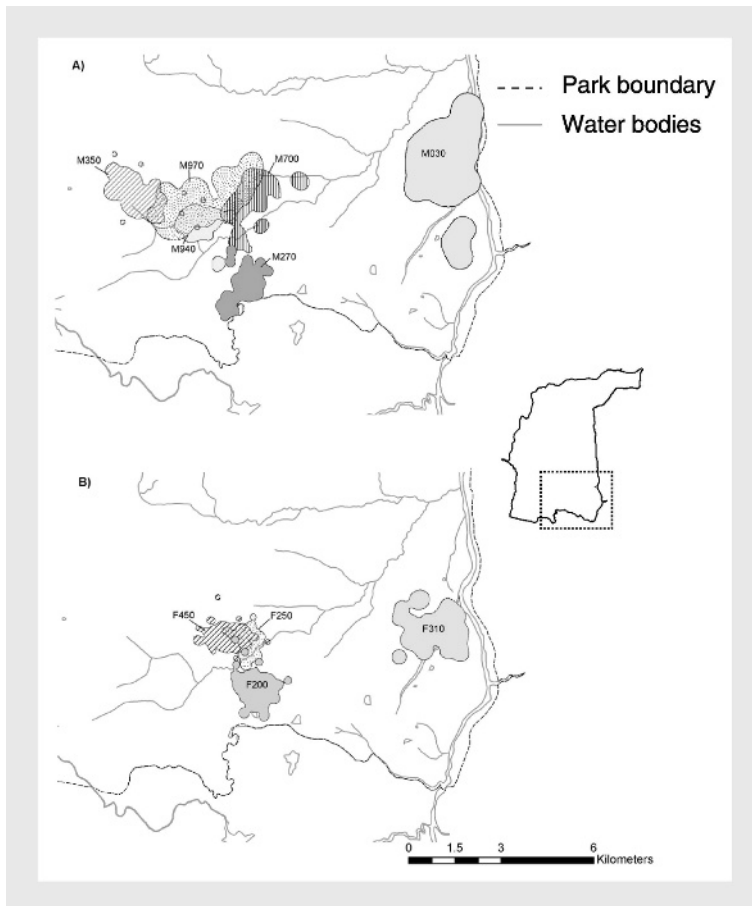

Figure 2. Fixed kernel (95%) home ranges of male (A) and female (B) sloth bears in Wasgomuwa National Park, Sri Lanka, during 2002-2003.

Results

Capture and telemetry

We radio-collared 10 adult bears (six males and four females; Table 2). All captured individuals were determined to be adult or nearly adult based on a combination of toothwear, mass (see Table 2), and reproductive characteristics. Bears # 450, 941 and 970 had extremely worn teeth; the nipples of all females, except # 250, showed evidence of previous litters, and bear # 200 was captured with a cub. Bears # 700 and 250 had the least toothwear and smallest body mass (see Table 2) for their sex and were probably young adults. We recovered the collar of male # 700 in April of 2003 at a recently occupied campsite of poachers. The bear probably was shot because the collar had been removed, carried to the campsite, and hidden under a log. We were not given access to continue our research during 2004, but wildlife staff found the carcass of a second adult male (# 030) in October near a national park road close to the boundary. They informed us that the bear probably had died as a result of a gun shot wound to the thigh.

We monitored the 10 bears for periods of 6-18 months from June 2002 to December 2003. All bears were monitored during the wet and dry seasons. We collected 647 locations by triangulation and 167 visual locations. The median telemetry error was 97 m (range: 12-1,117 m) based on 59 locations of test transmitters. Sloth bears were most active between 17:00 and 08:00 (Table 3) although we observed activity during other times of the day, particularly when ripe fruit of *Drypetes sepiaria* was available and during the rainy season, when daytime temperatures were lower.

Home ranges

Annual 95% fixed kernel home ranges of male sloth bears showed slightly more variation in size (CV = 65.7) than those of females (CV = 55.3). We did not detect a difference in home-range size between males and females (Mann Whitney U-test: P = 0.241; see Table 2), possibly because sample sizes of bears were small. Home ranges overlapped extensively within and between sexes (Fig. 2). Dry-season MCP home ranges were 1.3 times larger than wet-season home ranges (Wilcoxon test: N = 10, P = 0.020; Table 4).

Seasonal shifts in centers of activity of males ($\bar{x}$ = 0.51 km; range: 0.12-1.11 km, SE = 0.18) and females ($\bar{x}$ = 0.23 km; range: 0.10-0.33, SE = 0.05)

Table 4. Minimum convex polygon (MCP) and percent overlap of dry- and wet-season home ranges of male and female sloth bears, Wasgomuwa National Park, Sri Lanka, during 2002-2003.

Bear ID	No of locations Dry season	Wet season	MCP home range Dry season	Wet season	Percent of overlap among dry- and wet-season ranges
Males					
# 700	26	30	1.93	1.05	17.1
# 350	44	32	2.88	2.15	58.7
# 941	51	53	3.32	2.26	68.1
# 970	16	32	2.44	2.36	70.1
# 270	17	32	1.14	1.17	57.9
# 030	17	23	4.66	3.91	77.3
Mean			2.73	2.15	58.2
Females					
# 450	64	75	2.00	1.28	47.0
# 250	65	86	1.31	0.87	55.7
# 200	40	62	1.97	1.35	44.1
# 310	21	28	1.88	2.44	71.3
Mean			1.79	1.49	54.5

were small and did not differ between males and females (Mann-Whitney U-test: P = 0.594). Most bears simply expanded their movements during the dry season so the wet and dry-season home ranges overlapped considerably (see Table 4). Bear # 700 showed the most conspicuous shift in activity centers from the dry to the wet season. This shift seemed to be a result of short-range dispersal and settlement into a new area rather than an expansion of the home range; the resulting range was small, overlapping < 17.5% with his dry-season home range.

Habitat use

Kernel home ranges of sloth bears were situated within national park boundaries to almost complete exclusion of disturbed land, where levels of human activity were high (see Fig. 2). Although six bears had home ranges that were less than half a home range length from disturbed land, this habitat type comprised < 3% of sloth bear home ranges. Sloth bear use of habitat types differed from the composition within home ranges. Abandoned chenas were used less (upper 90% and 95% CI < 0.20), and high forest was used more (lower 90% and 95% CI > 0.20) than expected based on availability (Table 5). Telemetry error did not affect our analysis of habitat use within home ranges. When we incorporated telemetry error into our analysis of habitat use, the use of abandoned chenas was consistently less than expected and that of high forest was more than expected for all 10 replicates.

Table 5. Chesson selection indices (Chesson 1978, 1983) to determine habitat use within home ranges of sloth bears in Wasgomuwa National Park, Sri Lanka, during 2002-2003. Chesson selection index of 0.20 indicates habitat use in proportion to availability, < 0.20 = habitat use less than expected based on availability and > 0.20 = habitat use greater than expected based on availability. Habitat use was based on the proportion of locations in each habitat type within each bear's fixed kernel home range. All zeros were replaced with values of 0.001.

Bear ID	Denominator[a]	Abandoned chena	Secondary forest	High forest	Medium-high forest	Disturbed land
# 030 ♂	4.30	0.23	0.27	0.22	0.28	0.00
# 200 ♀	3.83	0.23	0.30	0.22	0.00	0.26
# 250 ♀	4.49	0.12	0.29	0.22	0.15	0.22
# 270 ♂	4.62	0.13	0.23	0.33	0.11	0.19
# 310 ♀	2.57	0.22	0.43	0.34	0.00	0.01
# 350 ♂	4.78	0.00	0.21	0.37	0.21	0.21
# 450 ♀	3.81	0.14	0.06	0.28	0.25	0.26
# 700 ♂	4.79	0.11	0.09	0.19	0.41	0.21
# 941 ♂	4.67	0.15	0.19	0.26	0.19	0.21
# 970 ♂	4.11	0.00	0.24	0.24	0.27	0.24
Mean		0.13	0.23	0.27	0.19	0.18
SD		0.08	0.10	0.06	0.13	0.10
SE		0.03	0.03	0.02	0.04	0.03
Lower 95% CI		0.081	0.165	0.228	0.109	0.122
Upper 95% CI		0.185	0.295	0.306	0.267	0.242

[a] See equation on page 276.

Discussion

Home ranges of sloth bears at Wasgomuwa National Park are among the smallest reported for any species of bear, matched only by an island population of American black bears *Ursus americanus* (Lindzey & Meslow 1977). Home ranges of mammals, including the Carnivora, are influenced by body size (McNab 1963, Gittleman & Harvey 1982, Gompper & Gittleman 1991), metabolic needs (McNab 1983) and the distribution and abundance of resources, such as food and mates (Macdonald 1983, Sandell 1989). Although we did not measure food distribution and abundance, we speculate that the small home ranges of sloth bears in our study area were a consequence of abundant and stable food sources, such as termites, which occurred in 61% of 660 sloth bear scats examined during the two years of our study. Termites also composed an average of 81% of scat volume during the wetter months (October through May). From June through September, the average composition of termites in scats dropped to 28%, the rest being composed mainly of fruit remains of *Drypetes sepiaria* and *Cassia fistula*.

We considered whether the small home ranges we observed were biased as a consequence of collecting locations primarily during time periods when bears were inactive. Sloth bears in Wasgomuwa National Park were most active during 17:00-08:00 (see Table 3), which corresponded with activity patterns of sloth bears in other portions of their range (Joshi et al. 1999). We collected 48% of our radio-locations during that time period so we conclude that our telemetry schedule did not bias the home-range estimates. Although home-range sizes among ursids show tremendous inter- and intra-specific variation, the few studies on sloth bears, sun bears *Helarctos malayanus* and giant pandas *Ailuropoda melanoleuca* indicate relatively small home ranges (Garshelis 2004).

Home ranges of male and female sloth bears at Chitwan National Park, Nepal, were 14.4 and 9.4 km[2] (MCP method), respectively. Those ranges are small in comparison with home ranges reported for American black bears and Asiatic black bears *U. thibetanus*, which are comparable in body mass to sloth bears on the Indian subcontinent (Joshi et al. 1995). The mean body mass of individuals captured in our study was approximately 66% of that of their counterparts in Chitwan National Park. Home-range sizes, however, represented about 25% of those reported for Chitwan National Park.

Sloth bears demonstrate a conspicuous departure from the general omnivore dentition that characterizes the Ursidae as a family through their specializations for myrmecophagy (Pocock 1933, Erdbrink 1953, Sacco & Van Valkenburgh 2004). Myrmecophagous mammals generally have smaller home ranges than other mammals of comparable body size (McNab 1983), either as a consequence of lower basal metabolic rates (McNab 1984), or

greater food abundance, or some combination of the two. Home ranges of the highly myrmecophagous South African aardvark *Orycteropus afer* (van Aarde et al. 1992, Taylor & Skinner 2003), are similar to those of *M. u. inornatus*, and both species have similar body sizes and basal metabolic rates (McNab 1992). Black bears and sloth bears also have similar basal metabolic rates, but home ranges of black bears are generally much larger (Garshelis 2004). The myrmecophagous habits of sloth bears and the abundance of food at Wasgomuwa are both likely explanations for the remarkably small home ranges we report. That smaller home ranges result from high food productivity or quality has been demonstrated across species (McNab 1963) and within species (Schaller 1972, Gompper & Gittleman 1991, Dahle & Swenson 2003); for example, Thompson et al. (2005) report very small home ranges (of 4.3 km^2) for female black bears in an agriculturally productive area. In general, insectivorous carnivores typically have small home ranges (Gittleman & Harvey 1982) presumably because protein-rich insect prey, especially ants and termites, are abundant and ubiquitous over relatively small areas (e.g. Wood & Sands 1978, Redford 1987).

The ability of sloth bears to forage efficiently on abundant and relatively stable insect foods and to subsist opportunistically on seasonally available fruit (Laurie & Seidensticker 1977, Gokula et al. 1995, Baskaran et al. 1997, Joshi et al. 1997, Bargali et al. 2004) may facilitate conservation efforts. Except for the fruit-producing tree *Cassia fistula*, whose ripe pods were available for a long period (May-October), the majority of fruits consumed by sloth bears in our study area ripened during the dry season (June-August). The most important fruit during the dry season was *Drypetes sepiaria* (weera), a dominant canopy species (Jayasingham & Vivekanantharajah 1994) whose stem densities may exceed 300 individuals/ha and occurred in all forest types of the study area (Pabla et al. 1998). The high proportion of fruit seeds observed in scats during June-August suggests that dry-season home ranges were larger because bears were exploiting patches of ripening fruit, which were possibly more dispersed in space than termite colonies.

Home ranges of sloth bears at Wasgomuwa National Park were almost exclusively within the national park boundaries, where human access was restricted. The tendency for sloth bears to avoid areas used by humans also was observed in Nepal. Sloth bears were rare or absent in areas used fre-

quently by humans (Garshelis et al. 1999b), and Joshi et al. (1995) observed that radio-collared sloth bears at Royal Chitwan National Park rarely ventured outside its boundaries. At Wasgomuwa National Park, the river on the eastern boundary probably was not a physical barrier to bear movements because park staff and villagers regularly waded across the river, except during peak monsoon rains. Villagers that lived on the east and south boundaries of the national park reported that sign of sloth bears was rare. We obtained two accounts of sloth bears visiting fields or streams close to villages at the boundary of the national park in 1985 and 1992, the former resulting in a woman being attacked and injured. Villagers killed both bears. For bears wandering beyond the national park boundaries, therefore, the probability of mortality is potentially high. It is noteworthy that a female sloth bear whose home range overlapped with the park's headquarters, and a male whose home range included a park bungalow, occasionally foraged or slept close to (< 100 m) these buildings. These observations suggest that sloth bears may habituate to human presence when it is non-threatening.

Assessing which habitats are selected by animals can often provide fundamental clues to how individuals meet their needs for survival and reproductive success. We hypothesized that differences in the amount of food or cover provided by the habitat types comprising the home ranges of sloth bears influenced sloth bear habitat use at the third-order level. Medium-high forests had been subjected to selective logging in the past and consequently had fewer large trees, but the semi-open canopy allowed for dense thickets of cover and a relatively dry ground layer (Pabla et al. 1998). Secondary forests had fewer large trees than high or medium-high forests and greater densities of thorny shrubs that formed thickets. Compared to the other vegetation types within the park, high forests at Wasgomuwa National Park have had the least anthropogenic disturbance in the previous four decades. The closed canopy permitted less vegetative growth at the ground level, but comprised larger trees (Jayasingham & Vivekanantharaja 1994) that presumably produced more fruit and had more den cavities. High forests had a comparatively moist ground layer due to low light penetration, providing better conditions for decomposers and nutrient recycling (Pabla et al. 1998). For sloth bears, the moist soil conditions could facilitate foraging for termites, and support a conceivably high abundance of ter-

mites. It is therefore not surprising that high forests were used more than expected.

Abandoned chenas result from shifting cultivation during previous decades and provided the least cover, consisting mostly of open areas (short grassland or fields) intercepted with patches of scrub. Within home ranges, sloth bears tended to use abandoned chenas less than expected, which may be related to the amount of vertical cover. Establishing why animals use particular habitats less frequently and whether infrequent use implies avoidance is desirable, but not always achievable (Garshelis 2000). Our data indicate that some sloth bears had small home ranges (≈ 2 km^2), despite a large proportion of abandoned chenas (30-45%). Thus, this habitat type may provide some valuable resources for bears. The bears in our study confined their use of abandoned chenas mostly to the patches of dense scrub scattered throughout these short grasslands. The open grasslands of abandoned chenas may provide little protection from high daytime temperatures. Indeed, the few occasions during which we observed bears in those grasslands occurred at night, but bears immediately responded to our presence by running to the nearest patch of scrub or forest. These observations suggest that the cover afforded by taller vegetation may provide some measure of safety and, when temperatures are high, shade. Termites are abundant in grasslands (Lee & Wood 1971), and tall grasslands are used extensively by sloth bears in some portions of their range (e.g. Joshi et al. 1995, Desai et al. 1997). It is possible that the vegetation structure of tall grasses provided more cover and shade than the short grasslands of abandoned chenas at Wasgomuwa National Park.

Conservation implications

The presence of adequate vegetative cover appears to be important for sloth bears, who used most major habitat types within Wasgomuwa National Park, including abandoned chenas, although use of the latter seemed to depend largely on the availability of dense patches of cover afforded by plant genera such as *Bauhinia, Premna*, *Lantana*, *Phyllanthes* and *Zizyphus*. In a study in North Bilaspur Forest Division, India, Akhtar et al. (2004) also documented less bear sign in areas relatively devoid of vegetative cover. Current habitat management in national parks in Sri Lanka is focused on improving grasslands for elephants by removing scrub species to improve the production of fodder. Balancing the fodder requirements of herbivores with the need for adequate cover by bears and other carnivores will make those habitats more attractive to a diversity of wildlife. The same argument applies to maintaining forest and scrub cover in travel corridors, which have been implemented to facilitate the movement of elephants among protected areas, if they are to be used by sloth bears. Because a system of protected lands and corridors is in place in Sri Lanka for the protection of elephants, relatively minor changes in habitat management of those areas may also prove extremely valuable for sloth bears.

Plant tissue is either directly or indirectly the source of food for termites (Lee & Wood 1971), thus soil and climatic conditions favouring high vegetation biomass and productivity may influence termite abundance across many types of habitat. High forests outside protected areas in Sri Lanka are likely to disappear as human populations expand and the need for land and timber increases, but if forest habitats with high plant biomass and vegetative cover exist, they may support healthy sloth bear populations. For example, Joshi et al. (1995) suggested that alluvial grasslands and sal forests in Nepal were valuable habitats for sloth bears because they provided an abundance of ants and termites.

Home-range size in carnivores tends to vary inversely with population density (Sandell 1989, Dahle & Swenson 2003). The small home ranges that we observed may be indicative of high sloth bear densities, indicating that relatively small protected areas ($\approx 40,000$ ha) may effectively conserve sloth bears, as long as human access is strictly regulated. In the absence of any population estimates for Sri Lanka, Santiapillai & Santiapillai (1990) tentatively reported a population estimate of 300-600 bears based on a crude density estimate of 5 bears/100 km^2. Given the home-range sizes of sloth bears we observed, Wasgomuwa National Park alone may support more than 100-150 sloth bears, particularly since home ranges showed substantial overlap and unmarked bears were frequently sighted within the home ranges of radio-collared bears (S. Ratnayeke, unpubl. data). Of course, such estimates should be interpreted with caution (Garshelis et al. 1999a), but the point we wish to make is that Wasgomuwa National Park comprises < 5% of sloth bear habitat in Sri Lanka. Many dry zone habitats comparable to Wasgomuwa National Park exist in Sri Lanka. Therefore, a maximum estimate of 600 sloth bears may considerably underestimate actual population abundance.

Joshi et al. (1995) speculated that the high survival of sloth bears within Royal Chitwan National Park in Nepal was partly a consequence of their small home ranges, resulting in fewer encounters with humans. In this study, we lost two adult males evidently from poaching activity within the national park. The home range of one of those males abutted the park boundary and was also the largest home range we observed. In Sri Lanka, most poaching activity involves procuring meat from herbivores, but sloth bears are incidentally killed, possibly because they pose a real or perceived threat when encountered. We encountered armed poachers on two occasions while radio-tracking on foot and observed abundant sign of poaching activity within the national park throughout the study. It seems that the greatest threat to sloth bears at Wasgomuwa National Park may come from illegal activities. A nation-wide survey conducted by our research team suggests that this pattern is typical of many protected areas in Sri Lanka (S. Ratnayeke, unpubl. data).

In Sri Lanka, rural villagers regard the sloth bear as symbolic of wilderness removed from humans, reflecting the uneasy relationship between man and sloth bear (e.g. Phillips 1984, Garshelis et al. 1999b, Rajpurohit & Krausman 2000; K. Yoganand, pers. comm.). Undoubtedly, this is partly because the range of sloth bears occurs within some of the most densely populated areas of the world so the opportunity for human-bear conflicts is high. The tendency of sloth bears to raid crops or use areas close to human dwellings is still rare in Sri Lanka. However, Akhtar et al. (2004) reported frequent human-sloth bear conflicts involving injuries to humans close to human dwellings, partly as a result of bears raiding agricultural fields. Similar examples of nuisance behaviour occur in other areas of India, where habitats have been destroyed or are so degraded that sloth bears seek resources outside natural forests, or the bear population simply dwindles and disappears (Garshelis et al. 1999b). Despite the advantage of their insectivorous diet and ability to use a wide range of habitats, sloth bears seem sensitive to human disturbance (Garshelis et al. 1999b) making them extremely vulnerable to habitat loss and fragmentation. Thus, conservation of existing sloth bear populations in Sri Lanka will require protected areas and the effective regulation of human activity within them.

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