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A review of studies on brown bear (*Ursus arctos*) ecology in relation to home range, habitat selection, activity patterns, social organisation, life histories and population dynamics

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Introduction

What is home range and why measure it?

In order to survive, terrestrial vertebrates require resources including food, water, cover and nesting or denning sites. Changes in the abundance and distribution of animal populations as well as in the home range and movements of individuals over time and space are often related to the varying availability of such life requisites (Litvaitis *et al.* 1996), as well as the effects of human activities (Truett *et al.* 1996). The home range of an animal has been defined as the „area traversed by the individual in its normal activities of food gathering, mating and caring for yong“ (Burt 1943 cited in Powell 2000). It is implicit in this definition that home range studies have the potential to provide significant insight not only into the size of area that individual animals utilise and the patterns of their movements, but also information on habitat use and selection, foraging strategies and diet, social organisation and interactions, mating patterns and reproduction, limiting resources and more (Powell 2000). Familiarity and use are both elements of home range. However, Burt´ s definition is vague and hence leaves considerable scope for variation in interpretation and understanding. No consensus exists for a single, precise definition of home range and no single method of measurement is best for all research(Powell 2000).

According to Litvaitis *et al.* (1996), the distributions of food and cover are likely to most influence the movements of an individual within its home range, although there may be other factors operating such as avoidance of competition. Herrero (1985:161) stated that seeking and eating food are the main motivators influencing the movements and locations of brown bears (*Ursus arctos*) and black bears (*Ursus americanus*). Movements and activity patterns of sloth bears in fragmented habitats in India were largely governed by phenological patterns of food plants, crop stages, food availability and disturbance factors as well as livestock grazing (Chauhan 2002). Knowledge of home range, movements and activity patterns therefore gives insights into a species habitat requirements as well as relations with humans and human activities, which can be used to prioritise areas for conservation (cf. Peralvo and Cuesta 2002). The selection and use of *habitat* (definet as including all abiotic and biotic features; see Garshelis (2000) for alternative definitions) are the result of proximate and ultimate factors. The former are cues used by animals to assess habitat, including stuctural features, canopy height, slope and presence/absence of potential competitors. Ultimate factors are those which have resulted in evolutionary associations between animals and habitat by determining how successful a species is within a particular habitat. They include an individual's abilities to obtain food, avoid predators and reproduce. Proximate factors are easier to measure in many instances, but assumptions about animal-habitat relatiionships should be tested. Patch size, corridors and degree of isolation may have important influences on population size and community structure (Forman and Godron 1986 cited in Anderson and Gutzwiller 1996) as well as movements of individual animals. Studying home range, movements, activity patterns, reproduction rates and survival can indicate the degree and nature of human activities impacting on individual bears and bear populations (e.g. Adamič 1997, Reynolds *et al.* 2002).

Home range, territory and population dynamics

Slovak authors have generally assumed that " bear trees", bitten into and rubbed on by Bears, are evidence that adult male brown bears maintain territories (Jamnický 1987, Baláž 2002). Sabadoš and Šimiak (1981) stated that a territory was maintained only during the breeding season. Some claim that dominant adult males "push" other bears out of prime habitat (e.g. Jamnický 1988, 2003, Kováč 1996, 2003, Rakyta 2001, Hell 2003). The argument has been used to support calls for changes in hunting that would allow the Legal hunting of larger bears (more lucrative financially and valuable for their trophies). The implication being that this would make more prime habitat available to less dominant bears and so reduce bear-human conflicts. Others (e.g. Baláž 2003) have taken an opposite view, claiming that dominant males play a significant role in population regulation, e.g. through their occasional killing of cubs and subadults (cf. Kováč 1999), and that their presence therefore limits population growth and hence bear-human conflicts. In North America, removal of adult males has generally been regarded as a possible strategy to increase, not decrease, bear density in order to maximise sustainble hunting yield (Taylor 1994, Sargeant and Ruff 2001)

Mechanisms of population regulation in bears are not well understood (Taylor 1994). Murie (1985: 75) concluded from his numerous observations of bear interactions, spacing and occasional intraspecific killing (sometimes predatory, particularly by large males on small cubs during the breeding season), that grizzly bear populations might have a tendency to be self-regulating. Studies of the Scandinavian bear population found decreased cub survivorship following selective removal of adult males, which it was suggested was due to sexually selected infanticide (Swenson *et al.* 1997, 2001a,b). However, Miller *et al.* (2003) found that in heavily hunted populations of brown bears in Alaska cub survivorship was higher and litter sizes were larger or unchanged compared to nearby unhunted populations thought to be near carrying capacity. These authors concludet that desity – dependent effects influenced cub survivorship only in populations near carrying capacity. Bear habitat in the Western Carpathians is generally assumed to be saturated (Hell and Fiďo 1999, Swenson *et al. 2000,* Zedrosser *et al. 2001*), so the Alaskan model is probably the more pertinent at the present time. Slovakia's bear population, presumably at or near carrying capacity and yet not particularly intensively hunted in recent years (Kassa 2003), could present a rare and valuable opportunity to investigate possible density- dependent responses.

The idea that bears might use "bear trees" to signal their presence and size to other bears was proposed by Seton (1929 cited in Murie 1961, 1985). However, in Mount McKinley (now Denali) National Park, Alaska, Murie (1961: 52-54) observed both male and female brown (grizzly) bears and black bears of a variety of ages rubbing their backs, sides, stomachs, rears and heads against such trees. Using DNA analysis, Kendall *et al.* (2002) found that 66% of individual grizzly bears identified from hairs left on "bear trees" were male. Murie felt that any scratching and biting of the tree during this activity was inicidental, the primary and conscious purpose being to massage itches. However, MacHutchon (2001) observed "marking behaviour" by both lone female and male grizzly bears. Becaus it was only seen during spring and summer, peaking from mid-May to early July, he concluded that it was associated with breeding activities.

Murie (1985: 2-78) was emphatic that grizzly bears do not maintain territories, having observed directly numerous instances of joint occupation of range, although he did recognize a dominance hierarchy in which smaller bears generally avoided larger ones. Huber and Roth (1993) reported over – lapping home ranges and no obvious territoriality among 26 radio - collared bears in Croatia to Murie's observations, some bears used the same area year-round if offered them sufficient food, whereas other individuals and family groups used different areas according to season. Some individuals used an area 1-2 miles in diameter (1-3 km) for several weeks. There were differences in habitat use among years. For example, bears tended to wander more widely if the berry crop failed, although generally still within their usual home ranges as observed in other years. Although, in general, bears had a strong tendency to occupy definite home ranges year to year, some were observed to shift ranges from one year to another.

The degree of territoriality in a given species may vary between areas and be related to food availability or other limiting factors (Powell 2000). Home range overlap, whether or not the animals concerned affect each other's behaviour and the degree of territoriality can be quantified in several ways (reviewed in Powell 2000). For exemple, Mace and Waller (1997) quantified the degree of overlap of grizzly bear home ranges in Montana. Swenson *et al.* (2000) noted that radio – telemetry studies in Europe have indicated extensive overlap in home ranges estimated by the minimum convex polygon method (cf. Huber and Roth 1993), although they felt that the real overlap in more concentrated activity areas was less known. Brown bears certainly do congregate at abundant food sources. Murie (1985: 62) observed short-term congregations of grizzly bears in areas of high food abundance, without notable conflict among them e.g. at least 23 bears, including five family groups and ≥6 lone bears, used an area of c.70 km¸ for most of a summer. In an extreme (human-induced) case, up to 70 individuals were seen during one night feeding at the same refuse dump in Yellowstone National Park (Herrero 1985, Stringham 1986). Grizzly bears have been recorded traveling over 38 km from backcountry den sites in Banff National Park to reach refuse dumps (Herrero 1985) McNeil River Falls, Alaska, are famous for concentrations of bears during salmon runs. In such cases, dominant individuals appear to occupy prime sites, i.e. use dumps with less human activity and usurp the best fishing spots (Herrero 1985: 207-228).

Generally, bears avoid confrontation by a limited hierarchical organization and mutual avoidance. Avoidance may range from a few metres, as when fishing for abundant salmon, to several hundred metres when feeding on lush vegetation on the same meadow. Most encounters involve mutual assessment, sometimes with threatening behaviour and displays of dominance or submission, followed by withdrawal of the weaker bear, and only occasionally result in conflict. Mueller *et al.* (2004) found significant differences in the spatial distribution of adult and subadult brown (grizzly) bears on a larger scale in relation to habitat quality and human activity in Banff National Park, possibly due to intraspecific avoidance (cf. Van Horne 1982). These authors nevertheless acknowledged that their results could be explained by at least one other hypothesis, that bears nearer areas of high human activity are more likely to be killed before becoming adults. See reviews in Mattson 1990, Taylor 1994.

Why use telemetry?

Research on shy, nocturnal and forest-dwelling animals with large home ranges has been greatly facilitated by radio-telemetry (Kacyensky *et al.* 2002). Being able to recognize, follow and observe known individuals allows a wide range of data to be gathered in addition to estimating home range size. Bear biologists use radio-telemetry to estimate habitat use and selection, bear distribution, behaviour, frequency and size of litters, dispersal of juveniles and subadults, survival as well as emigration patterns

(Swenson *et al.* 2001a, Klenzendorf and Vaughan 2002, Lee and Vaughan 2003). On the individual level, bear response to humans has been studied using telemetry (Naves *et al.* 2001). Radio – telemetry has revealed various differences among individuals and groups in the same population, such as age-sex cohorts responsible for most predation on livestock (Knight and Judd 1983, Anderson *et al.* 2002). Recapturing marked bears allow monitoring of body condition at different times and, if the first capture was of a young animal, of growth rates in the wild (cf. Kaczensky *et al.* 2002).

Tracking bears by telemetry has facilitated studies of denning ecology (e.g. Friebe *et al.* 2001, Haroldson *et al.* 2002b, Hightower *et al.* 2002), which has led to assessments of the vulnerability of denning bears to disturbance (Linnell *et al.* 2000, Podruzny *et al.* 2002) and could be used to plan hunting seasons to minimize the risk of creating orphaned cubs (cf. Hell 2003). Collars with motion sensitive switches(reset or tip) can improve studies on circadian, seasonal and annual patterns of activity among sex-age classes and are superior to relying on changes in location, tone or strength of signal to indicate movement/activity (Wagner *et al.* 2001). Telemetry has become a standard method to assess the effectiveness of cub rehabilitation (Maughan 2001, Clark *et al.* 2002a), population augmentation (Servheen *et al.* 1995, Rauer 1997, Zedrosser *et al.* 1999, Quenette *et al.* 2001) or reintroduction (e.g. Zedrosser *et al.* 1999, Clark *et al. 2002b,* Mustoni *et al. 2002)* as well as to monitor nuisance bears after capture and re-release, Whether on site or after transport (Miller and Ballard 1982, Schwartz *et al.* 2002b). Improved knowledge of bear movements, activity patterns and budgets can give insight into adaptive behaviour (MacHutchon 2001), the nature of bear-human relations, causes of conflicts, possible mitigation measures (e.g. Chauhan *et al.* 2002) and effectiveness of such measures(Fersterer *et al.* 2001). Understanding dispersal mechanisms leads to predictions of future geographic spread and hence can be used to plan for future bear presence and possible conflicts with human interests (cf. Swenson *et al.* 1998a).

On a broader scale, telemetry has been used to estimate the size, trend and distribution of bear populations (Swenson *et al.* 1994, Schwartz *et al.* 2002b). Marking animals and thus obtaining data on social structure, behaviour and reproduction provides important information for managers setting hunting quotas in line with conservation goals. Estimates of human-caused mortality are essential to monitoring and managing vulnerable populations (Cherry *et al.* 2002). Large-scale studies and meta-studies including many marked individuals have been used to model aspects of population dynamics such as reproductive senescence (Schwartz *et al.* 2002a), survival and maximum sustainable yield (Reynolds *et al.* 2002). The impact on bear populations of major environmental events such as human-induced disasters has been assessed (e.g. Sellers and Miller 1999). Conversely, base-line data on population dynamics collected prior to development can be used to identify and mitigate possible adverse effects of future human activities on bears (Reynolds *et al.* 2002). Radio-telemetry has also been used to assess research methods, such as investigating bias due to unequal "catchability" in mark-recapture population estimates (Noyce *et al.* 2001).

Materials and methods

Habitat use and selection

Various methods have been used to define and quantify relationships between animals and habitats (reviewed in Garshelis 2000, Litvaitis 2000, Powell 2000). In this context, it is important to distinguish between use, selection and preference. Use is taken to be selective if resources are exploited more than would be expected by chance (Johnson 1980 cited in Litvaitis *et al.* 1996). However, there are intrinsic ambiguities associated with the application of such concepts (Garshelis 2000). Although assessments of habitat use and selection are commonplace, many methodological difficulties are ofen overlooked (Garshelis 2000). For example, selection does not necessarily imply biological need and density is not always positively correlated with habitat quality. Van Horne (1982 cited in Litvaitis *et al.* 1996) found that subordinate (juvenile) deer mice (*Peromyscus maniculatus*) became locally abundant in "sink" habitats as a result of avoiding dominant individuals occupying "source" habitats with abundant food and cover. See Mueller *et al.* (2004) for possible evidence of a similar situation in bears.

Habitat selection (use versus availability) has been measured in three general ways:

1. by conducting an inventory of available habitat and comparing its composition to that of the animal's home range, of all individuals' home ranges combined or of the study area,
2. by comparing random samples to the characteristics of sites where use has been detected, often using logistic regression,
3. by establishing systematic plots and comparing those where use is detected to those where it is not.

Sites are usually sampled using a variety of techniques from plant ecology , forestry and range management (reviewed in Anderson and Gutzwiller 1996, Higgins *et al.* 1996).

Both direct and indirect methods have been used to record wildlife habitat use (reviewed in Litvaitis *et al.* 1996). Direct methods include observation (including of lead animals, e.g. Russell and Enns 2003), capture and radio-telemetry. For example, Onorato *et al.* (2003) compared vegetative associations at radio-locations to those within the estimated home range of the individual. Mueller *et al.* (2004) measured the distance of radio-locations from high quality habitat for different age-sex classes of brown bear. Indirect methods record evidence of animal activity within an area or at a specific site and include recording/counting tracks, faeces, feeding sites or nesting/denning sites. Such sign surveys can be used to estimate population abundance and quantify habitat use and availability (Cuesta *et al.* 2003). Akthar *et al.* (2004) recorded signs of use by sloth bears (*Melursus ursinus*) in different habitat types along established transects and compared the frequency of sign in each habitat type to the availability of habitat type in the study area as determined by sample plots.

General associations between animal species and habitat attributes can be obtained at a "macro" scale by using remotely acquired habitat data (e.g. from maps, aerial photographs, colour infrared photographs, satellite images or videography) and tools such as Geographic Information Systems (GIS) and Global Positioning Systems (GPS). See reviews in Koeln *et al.* 1996, Corsi *et al.* 2000). Several studies have used Landsat Thematic Mapper imagery to determine habitat type, with greenness taken as an indicator of habitat quality (Mace *et al.* 1999, Nielsen *et al.* 2002, Mueller *et al.* 2004 for N. America, Leacock 2003 for Kamchatka). Jones and Pelton (2003) used ArcInfo and GIS to determine macrohabitats associated with bear locations (as determined by radio-telemetry), determine proportions of available habitat and assess landscape-scale habitat selection. Mace and Waller (1996) compared grizzly bear telemetry coordinates to random coordinates, the latter being used to determine resource availability. Habitat classification by remote imagery is generally verified at sample plots directly in the field (e.g. Waller and Mace 1997).

Several major flaws have been identified in many habitat-related studies of wildlife (reviewed in Garshelis 2000). Many of these relate to difficulties in assessing habitat availability (and use) for use-availability comparisons. Scales of measurement directly influence results and their interpretation (Anderson and Gutzwiller 1996, Litvaitis *et al.* 1996, Garshelis 2000). Scales and environmental heterogeneity are continua, despite the convenience of considering discrete variables such as days, season, home ranges and geographic range. Information should be gathered at a scale comparable to that of the research or management question to be addressed. Habitat selection can occur at different scales, including the biogeographic (e.g. forested mountains in central Slovakia), home range (e.g. montane spruce forest and sub-alpine meadows) and activity point (e.g. den site). Different factors influence selection at each of these levels, e.g. climatic extremes might determine the geographic distribution of a species while habitat structure might influence home range size and shape. Habitats themselves can be characterised on different scales: on a "macro" scale according to the dominant biome or cover type (e.g. alpine meadow, coniferous forest) or on a "micro" scale (e.g. stem density, canopy closure). According to Bowers (1995 cited in Garshelis 2000), microhabitat selection and usage relates to individuals rather than species. Examining both scales may provide the greatest insight into animal-habitat relations (references in Litvaitis *et al.* 1996).

Home range size

Measurement of home range size and periphery is fraught with difficulties not acknowledged by many authors (Powell 2000). The methods, models and analyses used to estimate home ranges have considerable influence on the results obtained as well as on their interpretation. Familiarity with as well as use of habitat is important, but there is no agreement on how best to quantify an animal's familiarity with its surroundings (Powell 2000). Different parts of a home range may be used differentially and their relative use may vary over time. Time spent in different places is used by most researchers as an index of importance. However, a home range's contribution to fitness is ultimately of greatest importance, although is not so easily measured (Powell 2000). Areas or resources used only occasionally (e.g. water sources) may be vital to an animals whereas the importance of other areas used for long periods (e.g. resting/sleeping sites) might be over-emphasised in data sets.

Approximate homes ranges have been estimated by direct observations of recognizable individuals or family groups (Murie 1985), sometimes aided by capture and marking (Murray and Fuller 2000), with the implicit limitation that the bears must be seen and hence use of certain areas at night or in dense cover is likely to go unnoticed. Baláž (2002) measured the heights of bite marks on "bear trees" to estimate the home ranges of supposedly territorial adult males, but it is not clear that this is based on a valid premise (see above) and, in any case, packs of wolves (*Canis lupus*)-which certainly do seem to mark and defend territories (Mech 1970, Powell 2000)- occasionally make forays outside their territory, considerably increasing the totalarea used if they are included in home range estimates (W. Smietana pers. comm. 2003). Murie (1985:63) described cases of brown (grizzly) bears venturing warily beyond their usual home ranges. Snow-tracking, commonly used to assess wolf numbers and in some cases to delineate their home ranges (Boitani 2003), is obviously restricted in its applicability to studies o bears due to decreased activity during periods of snow cower as well as variation in habitat use at different times o year as bears forage for seasonally abudant plant and animal foods (cf. Mueller *et al.* 2004), but it has been used to estimate some bear populations in spring in Scandinavia (Elgmork 1996) and in early winter in Slovakia (Lehocky 2002).

Telemetry

Radio-telemetry avoids most of the problems discussed above and, as well providing the opportunity to follow annual patterns of known individuals, allows age/sex differences to be examined (cf. MacHutchon 2001, Mueller *et al.* 2004) and can also be used to obtain information on habitat components such as den sites. However, its level of accuracy may limit application in a patchy environment, it is expensive and sample size is usually small (Litvaitis *et al.*1996). Even telemetry does not lead to studies based on completely objective statistical methods (Powell 2000). Bears most be live-captured in order to fit transmitters (see Jonkel 1993 and Kaczensky *et al.* 2002 forrecommended procedures). Capture, immobilisation and handling may themselves bias results. Such effects have not been thoroughly assessed in most studies on vertebrates (Murray and Fuller 2000, Klenzendorf and Vaughan 2002). Moreover, these procedures are highly invasive and risk stressing, injuring and even killing the target animal as well as any others trapped unintentionally (cf. Kaczensky *et al.* 2002). Murie (1985:34) raised aesthetic objections to the capture and marking of animals in wilderness areas. Trapping and handling are also potentially hazardous to researchers as well as other people not directly involved but using the area, particularly if a cub is caught and its mother remains free nearby (Kaczensky *et al.* 2002).

Capture. Bears are commonly live-trapped with leg-hold snares (Johnson and Pelton 1980 cited in Wakkinen and Kasworm 2004) and Aldrich foot snares (Lee and Vaughan 2003 for N. America, Swryodkin *et al.* 2003 for the Russian Far East). In Europe, snares are regarded as non-selective traps and so their use may be problematic due to legislation (Kaszensky *et al.* 2002). Nevertheless, they have been used (e.g. Naves *et al.* 2001 in Spain). Huber and Roth (1993) used spring activated foot snares in Croatia and baited them with slaughterhouse refuse or animal carcasses. In Slovenia, Kaczensky *et al.* (2002) used Aldrich foot snares (2-6 per trap site) at established bait sites with carcasses, slaughter remains, corn and fruit. They considered them safe, selective and efficient in forested habitats. Barrel and culvert traps are also common in N. Amerca and elsewhere. Onorato *et al.* (2003) baited barrel traps for black bears in Texas with sardines and fish oil. Darting from a helicopter is very efficient and highly selective but is largely restricted to open habitats (McLoughlin *et al.* 1999, Miller *et al.* 2003). Free-range darting, e.g. from an elevated blind at a bait site during fuul moon, was rather inefficient in Slovenia and carried considerable risks for those involved, but was considered to have an application in special situations such as immobilizing a handicapped or human habituated individual or female next to her trapped young (Kaczensky *et al.* 2002). A baited cage was used to capture a nuisance bear in the Czech Republic (Barto3ov8 2003). Cages have also been used for the same purpose in Slovakia (Kováč 2003). In one case a net was used but the bear escaped (S. Ondruš pers. Comm. 2001). Hightower *et al.* (2002) trapped from April to September, Sellers and Miller (1999) darted bears in May and early June. Anderson *et al.* (2002) began trapping at lower elevations in June and moved upslope with seasonal snowmelt. Huber and Roth (1993) captured most bears in April-June, but also some in July and September-November. Due to hunting management practices and safety concerns during summer, Kaczensky *et al.* (2002) had two discrete trapping seasons: from snowmelt until mid-May and from October until the first heavy snowfall. They used an alarm system to minimise the time that a bear spent in a trap, recommending that handling should begin within 1-2 hours of capture. Bears were caught from 17.00 h to 01.00 h and from 03.00 to 08.00 h. For safety reasons, these authors recommended that trapping should be done at sites with vehicular access and at times when there is little likelihood of unexpected human visitation.

Chemical immobilization. To immobilize captured black bears, Onorato *at al.* (2003) used Telazol ® at a dosage of 5.5mg/kg administered via jabstick. For brown bears, Seryodkin *et al.* (2003) used a mixture of ketamine hydrochloride (7.2 mg/kg) and xylazine hydrochloride (3.6 mg/kg)or Telazol ® (same dose as ketamine). Huber and Roth (1993) administered ketamine and xylazine with a dart-gun or blow pipe. Kaczensky *et al.* (2002) mostly used a combination of tiletamine HCl and zolazepam HCl (Zoletil 100R, average 12.6 mg/kg body mass) administered by CO_2 dart gun and air-pressure activated dars and considered it very safe and reliable, although the recommended dose (5 mg/kg body mass) was found to be too small and recovery time was up to 8h due to the lack of a complete antagonist (in all cases, researchers stayed at the trap site until the bear woke up and left the area). Caulkett *et al.* (2002) tested four immobilizing drug combinations and concluded that the best choice was medetomidine-zolazepam-tiletamine, a combination used by the Scandinavian Brown Bear Research Project (Friebe *et al.* 2001; see Kaczensky *et al.* 2002 for alternate dosages and antagonists). Standard body measurements, hair and blood samples and a premolar (PMl) are usually taken from sedated bears (e.g. Kaczensky *et al.* 2002). Captured bears are usually marked with coloured plastic ear tags (e.g. Kaczensky *et al.* 2002) and sometimes also with lip tattoos (e.g. Sellers and Miller 1999).

Marking. Recent studies have marked bears with conventional (motion-sensitive, mortality-mode) VHF collars, VHF ear-tag transmitters (e.g. Mueller *et al.* 2004 for Banff National Park, Canada, P. Surth pers. comm.. 2005 for the Romanian Carpatian Mountains), satellite and GPS collars either with satellite uplink or store-on-board data collection systems (Arthur and Schwartz 1999, Schwartz and Arthur 1999, Belant 2002). Some studies fitted bears with radio-collars containing both a satellite telemetry transmitter and a VHF beacon (Arthur and Schwartz 1999, McLoughlin *et al.* 1999). In the case of ground locations obtained on conventional VHF collars, samples are often biased due to uneven accessibility of terrain and the difficulty of obtaining fixes at night or in bad weather and may fail to indicate some areas important to bears (Arthur and Schwartz 1999, Mueller *et al.* 2004). Possible limitations of GPS collars are frequent inability to obtain fixes, possible influences of vegetation, animal movement, terrain and cost (Schwartz and Arthur 1999). Nevertheless, they have several advantages over conventional or satellite collars (Obbard *et al.* 1998). Whereas Belant (2002) reported possible biases in locations obtained from GPS collars related to habitat types and collar orientation, Arthur and Swartz (1999) concluded that they improved the accuracy and precision of home range estimates over VHF collars, largely by providing larger samples of locations. For a capture-mark-resight population density estimate, Sellers and Miller (1999) glued conventional transmitters to the hair of the mid-dorsal hump. Kaczensky *et al.* (2002) used VHF collars for subadults and adults and VHF eartags or hair-mount transmitters for cubs and yearlings. They reported that the signal reception range and lifespan of eartag and hair-mount transmitters was much less than that of radio-collars in rugged terrain. A yearling male in Spain was tracked for five months using a hair-mounted transmitter (Naves *et al.* 2001). Friebe *et al* (2001) implanted transmitter in the body cavity of yearlings. Backpack transmitters are also available for use with brown bears (Anderson *et al.* 2002). Several manufacturers of telemetry equipment are listed in the Appendix. To prevent equipment loss, accidents or neck injuries due to ingrown collars and to allow battery renewal, data downloading or removal of equipment from animals at the end of a study, collars include breakaway devices or modifications (e.g. Huber and Roth 1993, Sellers and Miller 1999, Clark *et al.* 2002a, Kaczensky *et al.* 2002, Miller *et al.* 2003; see review in Garshelis and McLaughlin 1998) so that they fall off after some time (2 weeks to 26 months, Kaczensky *et al.* 2002) or bears are recaptured near the end of radio battery life (e.g. McLoughlin *et al.* 1999). None of the radio-collers used in Slovenia (Katczensky *et al.* 2002) failed before the expected life-spans of 24 and 36 months. These authors emphasised that, due to rapid growth, yearling bears and/or those < 70 kg should not be collared and that breakaway devices must be used for all males plus subadult females and females of uncertain age.

Relocation. Following release, marked bears can be relocated from an aircraft (Mech 1983, Friebe *et al.* 2001, Mueller *et al.* 2004) or from the groud using a portable receiver, roof-mounted omni-directional antenna or hand-held antenna (e.g. 2- or 3-element Yagi). Most studies attempt to relocate marked animals at least once per week. Intensive studies record ≥ 1 location/bear/day (e.g. Friebe *et al.* 2001, Mustoni *et al.* 2002). Jones and Pelton (2003) obtained locations 1-4 times per week but eliminated those collected < 20 hours apart from habitat analyses to minimize autocorrelation. To obtain a location, bearings taken from ≥ 2 positions are plotted on topographic maps or aerial photographs and locations recorded to the nearest 100 m (Mueller *et al.* 2004). Friebe *et al.* (2001) determined locations from ≥3 bearings. Onorato *et al.* (2003) obtained ≥ 2 azimuths in ≤ 20 minutes. Huygens *et al.* (2003) usually obtained at ≥ 3 azimuths in ≤ 30 minutes. Most bearings used to triangulate bear locations in Fersterer *et al.* study (2001) were collected in ≤ 10 minutes and < 1 km from the bear. They continued efforts to locate bears until all locations feel within 0.125km2 on a map. Naves *et al.* (2001) used LOCATE II software to determine locations from bearings. Jones and Pelton (2003) only used locations with bearings separated by > 45 (for 90% of locations by 60-120 and obtained in ≤5 minutes). Average error in taking bearings on a signal can be assessed by testing with radio-collars in known locations (reported errors are c.100-300m; Jones and Pelton 2003, Onorato *et al.* 2003, Mueller *et al.* 2004). Naves *et al.* (2001) found a mean discrepancy of 255m between locations estimated by triangulation and where bears were actually seen. Lee and Vaughan (2003) reported an error of 14 in taking bearings on radio signals. Geographical features can block direct signals an/or generate misleading reflected signals, especially in mountainous terrain. The best tracking conditions are when the antenna and receiver are in direct line of sigh (pers. obs.). More precise locations can be ensured by using the radio-signal to approach to 100 - 400 m from the bear and partially circling it, by visual observation or by locating tracks in the area where the radio signal was detected (Seryodkin *et al.* 2003). Studies investigating movements must avoid disturbing bears (cf. Naves *et al.* 2001).

Data analysis. Data from radio-telemetry represent a series of points (with some margin of error) at which the target animal was relocated. To estimate home range, typically a probability function is used to eliminate outliers or a certain (arbitrary) percentage of relocations with the assumption that this excludes occasional sallies outside the usual home range (Burt 1943, Powell 2000). Alternatively, a grid can be superimposed on the study area and home range represented as cells in which the animal is relocated (e.g. Doncaster and Macdonald 1991, 1996). The oldest and most common home range estimator, the minimum convex polygon (MPC), only crudely outlines homes ranges, probably inaccurately maps boundaries that are in any case unstable while ignoring the (often more important) details of the interior. Furthermore, it is susceptible to extreme date points and can incorporate large areas that are rarely or never used (reviewed in Powell 2000). Constructing a 95% minimum convex polygon (discarding the outlying 5% of data points) might exclude forays beyond the usual home range but does not solve the other problems. Various alternative models and estimators have been tried, each with inherent problems. Powell (2000) concluded that kernel density estimators are the best available estimators for home ranges, although they are also not without drawbacks. Adaptive kernel estimates performed slightly worse in tests than fixed kernel estimators. Food and other resources are generally patchily distributed and hence an animal would be expected to use some parts of its home range more than others. Various techniques, most of them arbitrary and subjective, have been developed to identify core areas of use. Powell (2000) described a method that is objective and data-dependent (i.e. related to the animals itself) rather than arbitrary. In published studies on bears, home ranges are commonly estimated using 95% fixed kernel or 95% minimum convex polygon together with 50% fixed kernel models to illustrate core area(s) of use, e.g. in ArcView (Lee and Vaughan 2003, Onorato *et al.* 2003) or CALHOME program (Jones and Pelton 2003). Onorato *et al.*(2003) analysed the home ranges of individuals monitored for > 50 days and that had > 24 relocations. Waller and Mace (1997) used CALHOME to calculate seasonal (spring, summer and autumn), multi-annual 95% adoptive kernel home ranges. They excluded short-term forays. Mean annual home ranges are also commonly reported as are such measures as mean and maximum distance traveled between consecutive daily relocations. Artur and Schwartz (1999) concluded that MCP models required > 60 locations and kernel models required > 80 locations to be accurate and precise.

Alternative/complementary methods

Analisis of DNA can determine species, gender and individual identity (Kendall *et al.* 2002). Its applications in bear research were reviewed by Paetkau and Strobeck (1998) and Waits (1999). Non-invasive genetic sampling has been used to monitor bear populations. Several genetic studies on European brown bears have been published based on analyses of samples from hair and faeces (Taberlet and Bouvet 1994, Kohn *et al.* 1995, Taberlet *et al.* 1995, 1997, Kohn and Knauer 1998, Waits *et al. 2000,* Kruckenhauser *et al.* 2002). DNA microsatellite markers have been used to identify individual bears from scat and hair samples and hence estimate population numbers using mark-recapture techniques (Vowels *et al.* 2002) or the minimum number of bears using a particular area in a given period (Haraldson *et al.* 2002a). See Boulanger *et al.* (2002) for a comparison of study designs and Noyce *et al.* (2001) for an assessment of biases. Excremental PCR (amplification of DNA using polymerase chain reaction) has provided important data on demography, genetic variability, phylogeny and even food habits (Kohn and Knauer 1998). Genetic methods have also been used to assess population fragmentation (e.g. Proctor *et al.* 2002). Such a study in Slovakia and Poland might illuminate the consequences of a population bottleneck in the 1930s and genetic isolation of western and eastern sub-populations (see Kohn and Knauer 1998). Wills and Vaughan (2002) developed a project involving the use of DNA fingerprinting techniques to identify individual bears and their use of a travel corridor, hence assessing the extent of gene flow between bears in different geographic areas separating by anthropogenic barriers (see also Ruiz-García *et al.* 2002). They planned to place a 12 km-long strand of barbed wire 50 cm above the ground to capture hair samples from bears crossing it. Camera traps (baited, infrared activated) have also been use for mark-recapture population density estimation (e.g. Grogan and Lindzey 1999). Remonte cameras, infrared sensors and sand traps have been use to record movements at particular sites of interest such as "green bridges" (e.g. Huber *et al.* 2002). Sophisticated automatic monitoring stations (including video camera, directional microphone and weighing platform) installed at pre-existing feeding sites visited by bears were used successfully to assess the presence and biometric data of bears in a small popultion in the Italian Alps (Nicolini *et al.* 1997). Some individuals and family groups can be readily identified by an experienced field observer (e.g. Murie 1985). To facilitate future recognition, captured animals can be marked, for example with ear tags and tattoos, without fitting telemetry equipment (but cf. Murray and Fuller 2000). Sign surveys in combination with damage reports and verified oral testimonies were used to assess the distribution, population dynamics, habitat use, diet and relations with humans of a small relict population of bears in the Pyrenees in order to avoid exposing the bears to the risks of capture and immobilization (Caussimont and Herrero 1997, Camarra and Dubarry 1997, Parde 1997). Track counts along transects have been used to monitor cougar (*Puma concolor*) populations over a larger area. They are cheap, easily standardized, may provide a better index than hunting or damage data and do not require handling large numbers of animals as is necessary to estimate population size by telemetry, but would probably only detect relatively large changes reliably and efficiently (Smallwood and Fitzugh 1995, Beier and Cunningham 1996). Clevenger *et al.* (1997) combined location data from radio-collared bear with sign survey to evaluate bear habitat. Questionnaire surveys of game managers and conservation staff, supplemented or verified by fieldwork, have been used to obtain broad-scale information on distribution, approximate size and trend of populations about which few data are available (e.g. Chestin 1997 for Russia, Gula *et al.* 1998 for Poland).

European brown bear home range, movements, activity and social organization

Slovakia is one of the last countries in Europe with substantial numbers of bears in which radio-telemetry (and genetic research) has not been conducted. The following telemetry studies on European brown bears have been completed or are currently underway:

Country	**Bear population**[1]	**References**
Australia	Alps-Dinaric-Pindos	Rauer 1997, Zedrosser *et al.* 1999
Croatia	Alps-Dinaric-Pindos	Huber and Roth 1993, Huber *et al.*1996
Finland	North Eastern Europe	Kojola *et al.* 2002
France	Pyrenees	Camarra *et al.* 1998, Quenette *et al.* 2001
Greece and Bulgaria	Rila-Rodope	L. Georgiadis pers. comm. 2005
Italy	Appenine	Gentile *et al.* 1996
Italy	Southern Alps	Roth 1983, Mustoni *et al.* 2002
Poland	Carpathian	Jakubiec 2001
Romania	Carpathian	Mertens and Sandor 2000
Slovenia	Alps-Dinaric-Pindos	Kacyensky *et al.* 2002, Adamič 2003
Spain	Cantabrian	Clevenger *et al.* 1990, Naves *et al.* 2001
Sweden and Norway	Scandinavian	Swenson *et al.* 1994, Nygard *et al.* 2002

[1] Refers to genetically isolated populations destribed by Swenson *et al.* (2000), Zedrosser *et al.* (2001)

Typically for large carnivores, European brown bears occur at low desities, especially in northern populations (e.g. 0.5 bears/1,000 km^2, in south-eastern Norway, 20 - 25 bears/1,000 km^2, in an area of central Sweden, 100 - 200 bears/1,000 km^2, in Romania, references in table and Swenson *et al.* 2000; in forested mountains of Slovakia there seem to be c. 100 - 150 bears/1,000 km^2; Janík 1997, Rigg 2004) and have large home ranges. Home range size for adult males and females varies between areas, probably due to variation in food availability and distribution as well as population density (Swenson *et al.* 2000). For example, home ranges in core areas are 6-10 times greater in the Scandinavian boreal forest than in the productive forest of Croatia, where hard mast and feeding stations are available (Huber and Roth 1993). Crude estimates of the size of bear home ranges reported in Slovakia have generally been of c. 10 - 30 km^2, (e.g. Sabadoš and Śimiak 1981, Baláž 2002, 2003, Hell 2003). They tend to be derived by dividing the extend of occupied area by the estimated number of bears and thus are actually measures of density. Using these figures as home range estimates assumes that home ranges-even those of females and their own cubs-do not overlap at all, and thus in many if not most cases they are likely to be considerable underestimates. In Croatia, for example, 14 radio-collared bears were known to use an area of 736 km^2 (Huber and Roth 1993), equivalent to a mean home range of c. 53 km^2/bear if home ranges were not over-lapping. However, radio-telemetry showed that home ranges did over-lap; the four bears for which ≥ 17 daily locations were obtained used areas of 97-224 km^2 (minimum convex polygon). The mean home ranges recorded for four males and five females in Croatia were 128 km^2 (max.=224 km^2) and 58 km^2 (max.=147 km^2) respectively. The home ranges of males may have been even larger because they were harder to relocate (Huber and Roth 1993). As the apparent size of home ranges continued to increase for as long as additional relocations were obtained, these authors concluded that the concept of a finite home range was inapplicable to brown bears. Powell (2000) noted that ≥ 100 animal location estimates were needed to approach asymptotic values of home range area and outline using minimum convex polygons. Home ranges of hundreds and even thousand of square kilometers have been reported from elsewhere in Europe. An adult male in Bieszcxady, south-east Poland, used an area of 266 km^2, during a one-year period (Jakubiec 2001). Like those in Croatia, bears in Poland also made occasional forays for tens of kilometers beyond National Park boundaries (Z. Jakubiec pers. comm. 2005). Bears translocated from Slovenia used ranges in individual years estimated to total from 115 km^2 to 4,730 km^2, in the Austrian Alps (Rauer 1997, Zesrosser *et al.* 1999) and 796-1,233 km^2 in the French Pyrenees (Quenette *et al.* 2001). The two female bears released in the Pyrenees in May-June moved up to 52-55 km from the release site during initial exploration of their new surroundings before denning 2.7-6.6 km from the release site in late November. In central Sweden, home ranges of females averaged 225 km^2 and those of males 1,600km. Dispersing young males in Scandinavia may roam over areas up to 12,000 km^2 (Swenson *et al.* 2000). For comparison, 97 grizzly bears radio-tracked in Yellowstone National Park had average total home range sizes of 884 km^2, for females and 3,757 km^2, for males (Blanchard and Knight 1991). Annual range sizes differed by sex, age, reproductive status and amount of precipitation. Home range sizes of grizzly bears in Montana ranged from 34 km^2, for a subadult female to 1,114 km^2, for an adult male (Mace and Waller 1997). Barren-ground grizzly bears had mean annual ranges of 2,074 km^2, for females and 6,685 km^2, for males, at that time the largest recorded for grizzly bears in North America (McLoughlin *et al.* 1999).

Brown bears in Europe tp become more secretive and nocturnal than Siberian and North conditions, abundance of food, and human activity. Human persecution may have caused brown bears in Europe to become more secretive and nocturnal than Siberian and North American brown bears (Swenson *et al.* 2000). MacHutchon (2001) noted that brown bear activity budgets are highly variable geographically, seasonally and both among and within individuals, and may be influenced by individual traits (age, sex, weight, reproductive status and physiology) as well as environmental factors (weather, thermal stress, lunar phase, predation, seasonal food type and abundance, available daylight and human disturbance). In areas of low human use, brown bears are generally most active during the day and least active at night (reviewed in MacHudchon 2001). For example, grizzly bears in the Yukon tended to be more active during the day (especially morning and evening) than at night. They were active for 59-81% of the time, mainly foraging and feeding (MacHutchon 2001). In an area of higher human use, lone adults and family groups became more night-active or avoided the area, whereas subadults seemed to habituate to humans and remained day-active (MacHutchon *et al.* 1998). In the Slovak Carpathians, bears seem to be mostly night-active in areas of hair human use but are also active during daylight houses in areas of lower human use (pers. obs.). Bear activity patterns, movements and habitat use in the Cantabrian Mountains of Spain were significantly affected by human presence (Naves *et al.* 2001). Bears showed a strong preference for forest habitats, particularly mature hardwood forest, favoured lower elevations and avoided villages and roads (Clevenger *et al.* 1997). Bartošová (2003) noted the importance as refuges for bears of small primeval forest patches in the easternCzech Republik. Janík (1997) described road and forest track density as a limiting factor on bear use of habitat in Slovakia.

Median and maximum straight-line distance between consecutive day locations for radio-marked bears in Croatia (*n*=143) were 1.5 km and 8.5 km respectively. Average daily movements of males and females were similar, but females tended to confine theirs within a smaller area . The mean and maximum daily movements recorded from mid-May to late November in central Sweden were 3.4 km and 21 km respectively (Friebe *et al.* 2001). The resoective figures for a family group of bears in Spain from November to April were 0.55 km and 6.65 km (Naves *et al.* 2001). Most radio-collared bears in Croatiacrossed National Park boundaries. Bears traveled > 25 km beyond Park boundaries (mean = 10,4 km) and were relocated outside Parks 47-62% of the time (Huber and Roth 1993). Differences in the daily movements of individual bears were recognized in the Romanian Carpathian Mountains. Some individuals spent daylight hours within c. 1 km of refuse containers (P. Sürth pers. comm. 2005) while others traveled to them from forested mountains at distances of up to 15 km or more (Mertens and Sandor 2000) and to hunters' feeding stations from at least 17 km (Weber 1987). Interestingly, Fersterer *et al.* (2001) found that mean home range size of American black bears in supplementary feeding areas did not differ from that of bears in similar adjacent areas without supplementary. However, feeding stations did attract and concentrate bears at specific locations, bears seemed to alter their travel patterns to visit feeding stations and the same individuals often used more than such site in the same day.

Little is known about the social organization of brown bears, but the relationship among individuals, especially adults, depends largely on spacing and mutual avoidance except during the mating season (Swenson *et al.* 2000). Males tend to disperse more than females, which generally establish home ranges in or adjacent to their mothers' home range. However, extreme dispersal from the mother's home range has been documented in the expanding Scandinavian population (Swenson *et al.* 2000). Greater incidence and distance of dispersal, which promotes range expansion and gene flow, is associated with a positive growth rate in brown bear populations. Swenson *et al.* (1998b) reported evidence for pre-saturation dispersal from an expanding bear population in Scandinavia.

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