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Patterns of movement of released female brown bears in the Cantabrian Mountains, northwestern Spain

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Abstract: Between 2008 and 2013, 3 female brown bears (*Ursus arctos*; 2 cubs-of-the-year and 1 2-yr-old) were rescued, rehabilitated in captivity, radiotagged, and released back to the Cantabrian Mountains, northwestern Spain. We characterized their daily and seasonal movements post-release to gain insights into their movement strategies and the viability of bears released in human-dominated environments. The bears exhibited marked diurnal activity and were active throughout winter. Two bears demonstrated behaviors similar to those reported for wild bears, whereas one cub-of-the-year was recaptured after 21 days because she developed signs of habituation to humans.

Key words: bear release, brown bear, daily activity, movement, rhythms of activity, *Ursus arctos*

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Orphaned and injured bears have been captive-reared and released back into the wild for decades, often without a clear understanding of their adjustment to the wild and subsequent fate because post-release monitoring is not commonly practiced (van Dijk 2005, Huber 2010, Pop et al. 2012, Beecham et al. 2015). Beecham et al. (2015) demonstrated that the release of orphaned bears that were captive-reared is a justifiable management alternative because most were successfully returned to the wild. However, others consider this action undesirable (Huber 2005, 2010), mainly because of potential bear habituation to humans and associated human–bear conflicts (Herrero et al. 2005), which can affect human safety and public acceptance of bear conservation and agency management programs. Despite these concerns, we can expect that the number of bears that will be rescued and released will increase in the future as a consequence of increasing interactions between humans and wildlife, especially in human-dominated landscapes where brown bear (*Ursus arctos*) populations have recently increased (Chapron et al. 2014).

Information on the behavior of released individuals is important for bear management and conservation. In particular, characterizing individual movements may provide an important tool to understand bear behavior in response to the environment. Animal movements are the result of complex and dynamic patterns of space use resulting from daily activities associated with species' life histories, individual experience, and several intrinsic factors such as sex and age (Börger et al. 2006). The traits of each individual and its previous experience (as in the case of animals that have been injured, rescued, and then released) may influence the amount of time allocated to different behaviors (e.g., food acquisition and landscape exploration), thus affecting the properties of resultant movements. By understanding the relationship between individuals' movements and their environment, we can improve our knowledge of individual behavioral choices.

Our objective was to describe post-release movement patterns of 3 rehabilitated brown bears in the Cantabrian Mountains, northwestern Spain, at 4 temporal scales: diel, daily, monthly, and seasonal. Movement speed, total daily distance travelled, and diel displacements (e.g., night or day) can facilitate our understanding of individual behavior and how animals perceive their environment (Turchin 1998, Delgado and Penteriani 2008, Delgado

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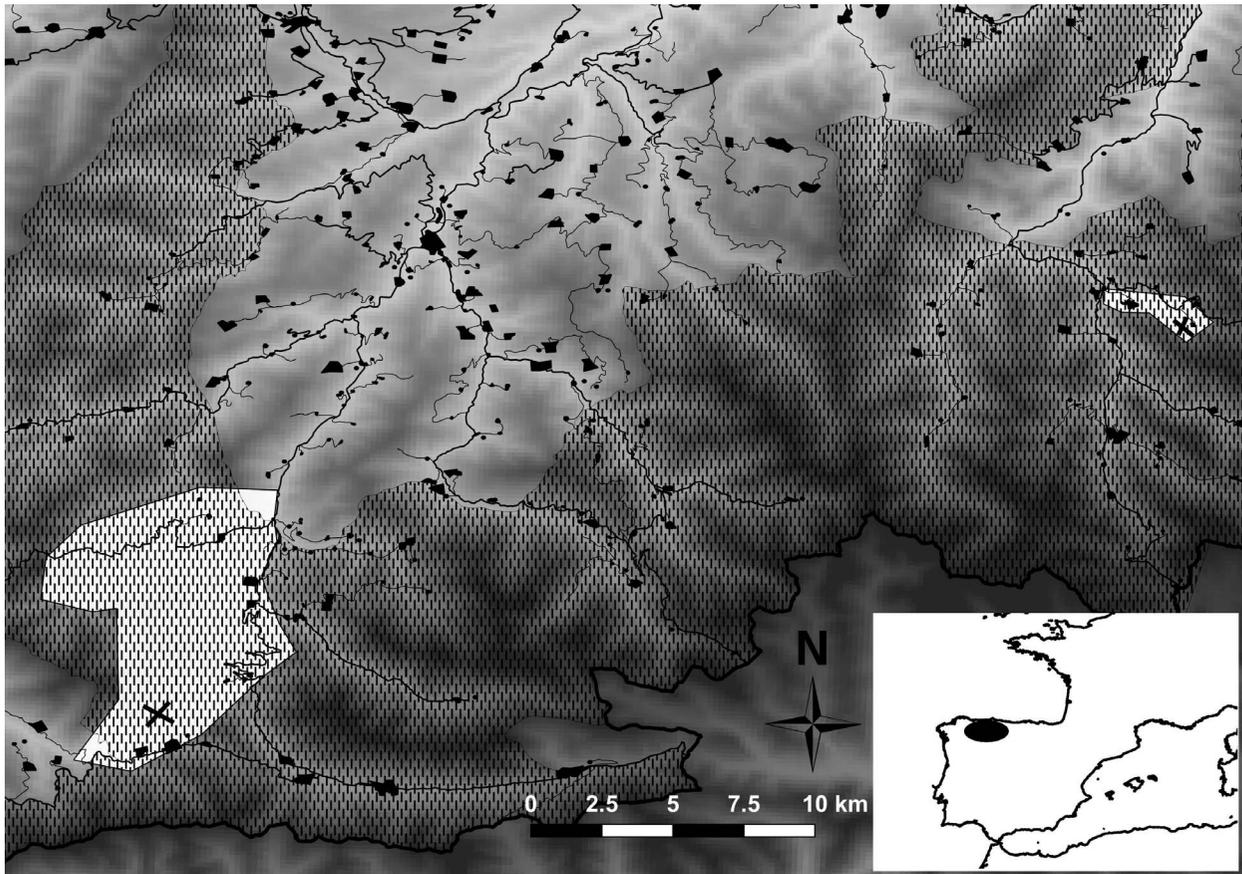


Fig. 1. The study area (Asturian Cantabrian Mountains of northwestern Spain) with human infrastructures (roads and human settlements, in black) and protected areas (grid pattern) around bear locations. Black crosses indicate release sites of brown bears (*Ursus arctos*) rescued, rehabilitated in captivity, radiotagged, and released between 2008 and 2013. One of the released females was only followed for <1 month and occupied the same area as another released bear, so only 2 of the 3 released females are shown (in white).

et al. 2010). Furthermore, we add to the limited body of knowledge of brown bears in the human-dominated landscapes of southern Europe (Clevenger et al. 1990, Naves et al. 2001, Mertzanis et al. 2005).

Methods

We recovered and released the 3 bears in the western Cantabrian Mountains (Fig. 1), a 300-km mountain range in northwestern Spain. Human population density is approximately 8/km² (Instituto Nacional de Estadística: <http://www.ine.es/jaxiT3/Datos.htm?t=2886>) and road density for the Asturias region, which contains the Cantabrian Mountains, is 47.4 km/100 km² (<http://www.seap.minhap.gob.es/index.html>). We

released the 3 bears within protected areas, 1.1–2.0 km from the nearest villages.

We rescued a cub-of-the-year (hereafter, female cub 1) on 26 June 2008 (approx. 5 months old and 3.2 kg) because of head injuries due to a fall or car accident. We released her on 11 November 2008 (wt = 28 kg) in the Natural Park of Somiedo (392 km²), Asturias, northwestern Spain (43°6'10"N, 6°15'5"W). The distance between rescue and release sites was 14 km. We equipped her with 2 very high frequency (VHF) transmitters (BIOTRACK TW-x tag, Wareham, England, UK; TINYLOC R2, Barcelona, Spain) and followed her daily for 239 days (through 7 Jul 2009). This female was alive on 19 September 2015 in Somiedo. We recorded 245 locations, so we provide estimates of home range only.

We rescued a 2-year-old subadult female on 7 April 2011 (approx. 15 months old) because of wounds possibly due to an adult bear attack (González-Quirós et al. 2015). We released her on 18 August 2012 in the Natural Reserve of Muniellos (55 km²), approximately 3 km from where she was found injured (43° 1' 16" N, 6° 42' 7" W). We determined her movements using a Global Positioning System (GPS) radiocollar (Model CRG 380 G, 450 g; Microsentry S.L., Cordoba, Spain) for 292 days until 5 June 2013, when the radiocollar fell off. We took locations every hour and recorded 3,701 locations. We last observed this female in Muniellos, and she has successfully reproduced as evidenced by the presence of one dependent young observed on 15 June 2016.

We rescued another cub-of-the-year (hereafter, female cub 2) on 19 September 2013 (approx. 9 months old and 6 kg) because of emaciation and head and femur injuries due to a fall. We released her 29 November 2013 (wt = 26 kg) in the same area where we released the subadult female in 2012, approximately 6 km from the location where she was rescued. We relocated her each hour using a GPS radiocollar (65 g Back GPS; Microsentry S.L.) for 21 days. We trapped her on 19 December 2013 after she repeatedly walked into villages during the day. We recorded 434 locations during this period.

Upon rescue, we kept all 3 bears in facilities for 41–145 days with minimal contact with humans except keepers and veterinarians, and with no enrichment programs. Immediately after rescue, bears were kept under veterinary care until recovery, when they were transferred to rescue centers until release. We fed the 2 cubs-of-the-year with moistened commercial food for dogs and isotonic drinks for 5–7 days, after which we fed them with fruits, nuts, and deer meat. The subadult female received fruits, nuts, and deer meat. We hard-released bears without supplemental feeding at the release site. The releases of both cubs-of-the-year occurred when they reached >6–7 months old, which is considered an age when self-sufficiency can occur (Loyal and LeRoux 1973, Swenson et al. 1998).

For the 2 bears with GPS collars, we describe post-release movements by estimating for each individual: (1) movement speed—the step distance (the distance between 2 successive locations) divided by the time interval between these 2 successive locations; (2) daily displacement—the straight-line distance between the first and last daily location of each individual; and (3) total daily distance—the sum of the step distances for each day. For diel movements, we defined diurnal as the time from sunrise to sunset and nocturnal from sunset to sunrise.

We calculated bear home ranges using ArcView 3.2 Geographic Information System software (Environmental Systems Research Institute, Redlands, California, USA). We estimated home range sizes for the subadult female and the female cub 1 only (because we only followed the female cub 2 for <1 month) using fixed-kernel methods (Worton 1989) and the Animal Movement Extension for ArcView 3.2 (Hooge and Eichenlaub 2000). We calculated 50% and 90% fixed kernels using least-squares cross-validation (Silverman 1986). We report means with ± 1 standard deviation.

Results

Subadult female (day: 247.8 ± 386.5 m/hr, $n = 1,954$; night: 159.9 ± 288.4 m/hr, $n = 1,742$) and female cub 2 (day: 202.6 ± 308.2 m/hr, $n = 280$; night: 179.7 ± 308.4 m/hr, $n = 149$) moved more rapidly during day than night. However, female cub 2 moved more at night, traveling 70.3% (57.9 km) of the total distance moved compared with the subadult female, who traveled 40.8% (30.5 km). Mean daily movement for the subadult female was 3.4 ± 1.9 km ($n = 281$ days), similar to that of female cub 2 ($\bar{x} = 3.9 \pm 2.0$ km, $n = 19$ days).

Average total distances moved for the subadult female were 3.6 ± 1.9 km in autumn (Aug–Nov), 3.1 ± 1.6 km in winter (Dec–Feb), and 3.7 ± 2.1 km in spring (Mar–May). The bears never entirely ceased their activity during the winter.

Mean monthly 50% and 90% fixed-kernel home-range size were 247.7 ± 200.8 ha (range = 23–659 ha) and $2,816.0 \pm 1,989.7$ ha (range = 634–7,698 ha) for the subadult female, and 47.9 ± 64.9 ha (range = 5–208 ha) and 181.6 ± 203.6 ha (range = 16–613 ha) for female cub 1, respectively.

Discussion

The subadult female and female cub 1 behaved similarly to wild bears, as observed by Beecham et al. (2015) for captive-reared American black bears (*U. americanus*) released into the wild. Indeed, movements and home ranges of the subadult female and female cub 1 were within the range of movements of wild-born, free-ranging brown bears elsewhere in Europe (Roth and Osti 1979; Roth 1983; Huber and Roth 1986, 1993; Clevenger et al. 1990; Palazón et al. 2012; Pop et al. 2012).

The greater diurnal movements of the subadult female did not follow the typical crepuscular or nightly activity of female bears recorded in the former Yugoslavia (Roth and Huber 1987), Sweden (Moe et al. 2007, Kindberg

2010), Greece (Mertzanis et al. 2005), and the Eastern Cantabrian Mountains (Clevenger et al. 1990). For example, brown bear movements were for the most part restricted to nocturnal and twilight hours in areas of Sweden with higher road densities, which is considered a good proxy for the influence of human activities on brown bears (Ordiz et al. 2014). However, we note that the subadult female's movements were restricted to within a protected area where human presence and disturbance were generally negligible, reducing the potential need to alter diel activity (Roth and Huber 1986, Ordiz et al. 2014). Further, dense forest cover may have contributed to the propensity for daytime activity. The subadult female's high rate of diurnal displacement is also typical of subadult individuals (Gau et al. 2004, Mueller et al. 2004, Nellemann et al. 2007).

The subadult female and female cub 1 were active in winter, though displacements were smaller than in spring and autumn, indicating that hibernation in the Cantabrian Mountains may be relatively short and predominantly coincide with snow and low temperatures (Nores et al. 2010, González-Quirós et al. 2015). The annual and local abundance of late autumn–winter food (hard mast from beeches [*Fagus sylvatica*] and oaks [*Quercus* sp.], as well as grasses and wild apples [*Malus* sp.]; Clevenger et al. 1990, Naves et al. 2006, Fernández-Gil 2013) may explain winter bear activity in the Cantabrian range.

Managers have 4 options when presented with an orphaned or injured bear: (1) leave it in the wild; (2) place it in permanent captivity; (3) euthanize it; or (4) place it in a captive-rearing facility for release into the wild (Beecham et al. 2015). Rehabilitation and release into the wild appeared appropriate for 2 of the 3 released individuals. Successful releases of orphaned or rehabilitated bears can have positive conservation implications including increased public support (Seddon et al. 2012), which is essential for the acceptance of large carnivores such as brown bears in the Cantabrian Mountains and necessary for positive coexistence between people and bears in human-dominated landscapes.

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Literature cited

- BEECHAM, J.J., M. DE GABRIEL HERNANDO, A.A. KARAMANLIDIS, R.A. BEAUSOLEIL, K. BURGUESS, D.-H. JEONG, M. BINKS, L. BEREZKY, N.V.K. ASHRAF, K. SKRIPOVA, L. RHODIN, J. AUGER, AND B.-K. LEE. 2015. Management implications for releasing orphaned, captive-reared bears back to the wild. *Journal of Wildlife Management* 79:1327–1336.
- BÖRGER, L., N. FRANCONI, N. FERRETTI, F. MESCHI, G. DE MICHELE, A. GANTZ, AND T. COULSON. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist* 168:471–485.
- CHAPRON, G., P. KACZENSKY, J.D.C. LINNELL, M. VON ARX, D. HUBER, H. ANDRÉN, J.V. LÓPEZ-BAO, M. ADAMEC, F. ÁLVARES, O. ANDERS, L. BALČIAUSKAS, V. BALYS, P. BEDÓ, F. BEGO, J.C. BLANCO, U. BREITENMOSER, H. BRØSETH, L. BUFKA, R. BUNIKYTE, P. CIUCCI, A. DUTSOV, T. ENGLER, C. FUXJÄGER, C. GROFF, K. HOLMALA, B. HOXHA, Y. ILIOPOULOS, O. IONESCU, J. JEREMIĆ, K. JERINA, G. KLUTH, F. KNAUER, I. KOJOLA, I. KOS, M. KROFEL, J. KUBALA, S. KUNOVAC, J. KUSAK, M. KUTAL, O. LIBERG, A. MAJIĆ, P. MÄNNIL, R. MANZ, E. MARBOUTIN, F. MARUCCO, D. MELOVSKI, K. MERSINI, Y. MERTZANIS, R.W. MYSLAJEK, S. NOWAK, J. ODDEN, J. OZOLINS, G. PALOMERO, M. PAUNOVIĆ, J. PERSSON, H. POTOČNIK, P.-Y. QUENETTE, G. RAUER, I. REINHARDT, R. RIGG, A. RYSER, V. SALVATORI, T. SKRBINŠEK, A. STOJANOV, J.E. SWENSON, L. SZEMETHY, A. TRAJČE, E. TSINGARSKA-SEDEFICHEVA, M. VÁŇA, R. VEEROJA, P. WABAKKEN, M. WÖLFL, S. WÖLFL, F. ZIMMERMANN, D. ZLATANOVA, AND L. BOITANI. 2015. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346:1517–1519.
- CLEVENGER, A.P., F.J. PURROY, AND M.R. PELTON. 1990. Movement and activity patterns of a European brown bear in the Cantabrian Mountains, Spain. *Bears: Their Biology and Management* 8:205–211.
- DELGADO, M.M., AND V. PENTERIANI. 2008. Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. *American Naturalist* 172:475–485.
- , ———, E. REVILLA, AND V.O. NAMS. 2010. The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology* 79:620–632.
- FERNÁNDEZ-GIL, A. 2013. Comportamiento y conservación de grandes carnívoros en ambientes humanizados. Osos y lobos en la Cordillera Cantábrica. Dissertation, Oviedo University, Spain. [In Spanish.]
- GAU, R., P. MCLOUGHLIN, R. CASE, H.D. CLUFF, R. MULDER, AND F. MESSIER. 2004. Movements of subadult male grizzly bears, *Ursus arctos*, in the central Canadian Arctic. *Canadian Field Naturalist* 118:239–242.

- GONZÁLEZ-QUIRÓS, P., J. MARCOS BELTRÁN, E. VIGÓN ÁLVAREZ, T. SÁNCHEZ COROMINAS, AND V.M. VÁZQUEZ. 2015. Selección del hábitat, movimientos y áreas de campeo de una hembra subadulta de oso pardo cantábrico, tras su recogida herida en el medio natural y su posterior liberación en una zona próxima a la de captura. *Boletín de Ciencias de la Naturaleza Real Instituto de Estudios Asturianos* 53:167–188. [In Spanish.]
- HERRERO, S., T. SMITH, T.D. DEBRUYN, K. GUNTHER, AND C.A. MATT. 2005. From the field: Brown bear habituation to people—Safety, risks, and benefits. *Wildlife Society Bulletin* 33:362–373.
- HOOGE, P.N., AND B. EICHENLAUB. 2000. Animal movement extension to ArcView, version 2.0. U.S. Geological Survey, Alaska Science Center - Biological Science Office, Anchorage, Alaska, USA.
- HUBER, D. 2005. Why not to re-introduce “rehabilitated” brown bears to the wild? Pages 28–34 in L. Kolter and J.J. van Dijk, editors. Rehabilitation and release of bears. Workshop on “The evaluation of bear rehabilitation projects from a conservationist’s point of view: Creating a linkage between different fields of interests.” The International Bear Foundation (Alertis) and the Bear Taxon Advisory Group (Bear TAG) of the European Association of Zoos and Aquariums (EAZA), November 2000, Zoologischer Garten Köln, Germany.
- . 2010. Rehabilitation and reintroduction of captive-reared bears: Feasibility and methodology for European brown bears *Ursus arctos*. *International Zoo Yearbook* 44:47–54.
- , AND H.U. ROTH. 1986. Home ranges and movements of brown bears in Plitvice National Park, Yugoslavia. *Proceedings of the International Conference on Bear Research and Management* 6:93–98.
- , AND ———. 1993. Movements of European brown bears in Croatia. *Acta Theoriologica* 38:151–159.
- KINDBERG, J. 2010. Monitoring and management of the Swedish brown bear (*Ursus arctos*). Population. Dissertation, Swedish University of Agricultural Sciences, Acta Universitatis Agriculturae Sueciae 58, Umeå, Sweden.
- LOYAL, J.J., AND P. LEROUX. 1973. Age of self-sufficiency in brown/grizzly bear in Alaska. *Journal of Wildlife Management* 37:122–123.
- MERTZANIS, Y., I. IOANNIS, A. MAVRIDIS, O. NIKOLAOU, S. RIEGLER, A. RIEGLER, AND A. TRAGOS. 2005. Movements, activity patterns and home range of a female brown bear (*Ursus arctos*, L.) in the Rodopi Mountain Range, Greece. *Belgian Journal of Zoology* 135:217–221.
- MOE, T.F., J. KINDBERG, I. JANSSON, AND J.E. SWENSON. 2007. Importance of diel behaviour when studying habitat selection: Examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology* 85:518–525.
- MUELLER, C., S. HERRERO, AND M.L. GIBEAU. 2004. Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15:35–47.
- NAVES, J., A. FERNANDEZ-GIL, AND M. DELIBES. 2001. Effects of recreation activities on a brown bear family group in Spain. *Ursus* 12:135–140.
- , ———, C. RODRÍGUEZ, AND M. DELIBES. 2006. Brown bear food habits at the border of its range: A long-term study. *Journal of Mammalogy* 87:899–908.
- NELLEMANN, C., S.O. STØEN, J. KINDBERG, J.E. SWENSON, I. VISTNES, G. ERICSSON, J. KATAJISTO, B. KALTENBORNE, J. MARTIN, AND A. ORDIZ. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138:157–165.
- NORES, C., F. BALLESTEROS, J.C. BLANCO, A. GARCÍA-SERRANO, J. HERRERO, AND G. PALOMERO. 2010. Evidence of non-hibernation in Cantabrian brown bears. *Acta Theriologica* 55:203–209.
- ORDIZ, A., J. KINDBERG, S. SÆBØ, J.E. SWENSON, AND O.-G. STØEN. 2014. Brown bear circadian behavior reveals human environmental encroachment. *Biological Conservation* 173:1–9.
- PALAZÓN, S., A. BATET, I. AFONSO, D. CAMPS, P.-Y. QUENETTE, F. DECALUWE, AND J. RUIZ-OLMO. 2012. Space use patterns and genetic contribution of a reintroduced male brown bear (*Ursus arctos*) in the Pyrenees between 1997 and 2011: The risk of genetic dominance of few males in reintroduced populations. *Galemys* 24:93–96.
- POP, I.M., A. SALLAY, L. BERECZKY, AND S. CHIRIAC. 2012. Land use and behavioral patterns of brown bears in the south-eastern Romanian Carpathian Mountains: A case study of relocated and rehabilitated individuals. *Procedia Environmental Sciences* 14:111–122.
- ROTH, H.U. 1983. Diel activity of a remnant population of European brown bears. *International Conference on Bear Research and Management* 5:223–229.
- , AND D. HUBER. 1986. Diel activity of brown bears in Plitvice Lakes National Park, Yugoslavia. *International Conference on Bear Research and Management* 6:177–182.
- , AND ———. 1987. Patterns of amount of activity of brown bears in Yugoslavia: Abstracts from the Third Congress of the Croatian Biological Society, Mali Losinj, Yugoslavia.
- , AND F. OSTI. 1979. Prime esperienze di radiolocalizzazione di due Orsi bruni del Trentino. *Natura Alpina* 30:27–38. [In Italian.]
- SEDDON, P.J., W.M. STRAUSS, AND J. INNES. 2012. Animal translocations: What are they and why do we do them? Pages 23–32 in J.G. Ewen, D.P. Armstrong, K.A. Parker, and P.J. Seddon, editors. *Reintroduction biology: Integrating science and management*. Wiley-Blackwell Publishing, Oxford, England, UK.
- SILVERMAN, B.W. 1986. Density estimation for statistics and data analysis. *Monographs on statistics and applied probability*. Chapman and Hall, London, England, UK.

- SWENSON, J.E., R. FRANZÉN, P. SEGERSTRÖM, AND F. SANDEGREN. 1998. On the age of self-sufficiency in Scandinavian brown bears. *Acta Theriologica* 43:213–218.
- TURCHIN, P. 1998. Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.
- VAN DIJK, J.J. 2005. Considerations for the rehabilitation and release of bears into the wild. Pages 7–16 in L. Kolter, and J.J. van Dijk, editors. Rehabilitation and release of bears. Workshop on “The evaluation of bear rehabilitation projects from a conservationist’s point of view: Creating a linkage

between different fields of interests.” The International Bear Foundation (Alertis) and the Bear Taxon Advisory Group (Bear TAG) of the European Association of Zoos and Aquariums (EAZA), November 2000, Zoologischer Garten Köln, Germany.

- WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70:164–168.

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