ACTA ZOOLOGICA BULGARICA

Acta Zool. Bulg., 73 (3), September 2021: 371-384

Terrestrial Ecology and Behaviour
Research Article

Published online 10 December 2020
http://www.acta-zoologica-bulgarica.eu/002476

Brown Bear Behavioural Response to Capture: Lessons Learned from a Small Sample

***Vladimir R. Todorov*[1,3*]*, Diana P. Zlatanova*[2] *& Kalina V. Valchinkova*[1]

[1] Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria; E-mail:vladimirtodorov.r@gmail.com, kvalchinkova@gmail.com
[2] Department of Zoology and Anthropology, Faculty of Biology, Sofia University "St. Kliment Ohridski", 8 Dragan Tsankov Blvd., 1164 Sofia, Bulgaria; E-mail: dianazlatanova@biofac.uni-sofia.bg
[3] Balkani Wildlife Society, 8 Dragan Tsankov Blvd., 1164 Sofia, Bulgaria

Abstract: Data from nine GPS-tracked bears from the poorly studied East Balkan population were used as a case study to assess brown bear risk-taking on approaching anthropogenic structures after being captured. We tested the hypothesis that, after capture and handling, the bears avoid places posing a risk of recapture. Two major effects were analysed: 1. Capture site effect, testing if bears tend to remember the capture location and avoid it as a threat for recapture, and 2. Feeding station effect, testing if the bears are avoiding the supplementary feeding stations as a potential threat for recapture. The avoidance of capture sites, as locations posing immediate risk of recapture due to animal's previous experience, was the highest (70% of all cases), followed by avoidance of feeding stations (60%). Thus, our study confirmed that the capture event had a significant impact on the animal behaviour and could be efficient tool (at least in short term) for managing unwanted bear behaviour. However, the results also showed that despite the capture event, bears did not entirely avoid the capture sites or the feeding stations. The males in our study were heterogeneous group in their avoidance behaviour, while females were showing strong avoidance of the two disturbance factors. Bears had very diverse response to the capture effect in respect of the distance they kept from the capture sites and feeding stations.

Key words: *Ursus arctos*; GPS telemetry; capture site; supplementary feeding stations; anthropogenic structures.

Introduction

The brown bear *Ursus arctos* L. is a large charismatic mammal with a conflicting nature of a predator. However, the species manages to live in human-dominated landscapes of Europe, forming several large and relatively stable populations (Chapron et al. 2014). A major focus for brown bear conservation on the continent is obtaining reliable scientific data on its numbers and density (Kaczensky et al. 2012). However, in many studies, key behavioural aspects are often omitted or neglected. Analyses based on *all* variables are needed to provide a strong scientific basis for solving the important for the bear conservation social conflict over knowledge and information (Linnell 2013). It is especially relevant for countries like Bulgaria where local people connect directly the bear population numbers to the damages on livestock, beehives and property, while most of those damages are done by few habituated

*Corresponding author: vladimirtodorov.r@gmail.com

bears. Effective sources of information in this aspect are the telemetry studies and recent versions like GPS and GPS/GSM are crucial. The advantage of the GPS telemetry is that it collects a large number of fixes (Cagnacci et al. 2010) and this high spatial resolution data provides valuable insight on the behavioural aspects of movement rate, activity patterns, home range size, habitat use, predation rate and interactions with anthropogenic food resources and infrastructure. It is particularly important in studying interactions with humans (e.g., in problem bears), where fine-scale movement data is greatly needed to either tackle conflicts or design plans for mitigation of barriers in ecological corridors (LCIE 2007, Linnell et al. 1998).

The capture of bears for telemetry studies is primarily executed in three ways: capture with leghold snares, remote sedating from stand or helicopter (helicopter darting) and barrel (culvert) traps (Arnemo & Fahlman 2007, Jerina et al. 2012, Jonkel 1993). Currently, the bear welfare during capture and release is of the highest importance, keeping the triple R concept in mind (Replacement, Reduction and Refinement) (Flecknell 2002, LCIE 2018, Smith 2001). However, a plethora of capture-related effects might go undetected and unanalysed.

Many published sources report that capture of a mammal for any purpose, especially tagging, is an invasive process, which might affect their behaviour and performance (Brivio et al. 2015, Chi et al. 1998, Moa et al. 2001, Northrup et al. 2014, Rode et al. 2014). Capturing with further handling by humans is likely to be one of the most stressful events in animal lives. This is proved in wild ungulates by studying haematological and biochemical values of blood samples (Spraker 1993, Wesson et al. 1979) or behavioural responses (Morellet et al. 2009). The only existing literature source for such a study in ursids is based on radio-telemetry data and has been focused only on the relationship between the effect of capture and body condition index, capture injuries and related mobility (Cattet et al. 2008). The potential of fine-scaled GPS-telemetry tracking for studying possible behavioural changes in the post-release period, such as abnormal mobility, changes in habitat use and possible reactions to human-induced disturbances is hardly used. Several published studies analysed the collared bears' interactions with human infrastructures, however, without an account of the capture effect. These results showed that the interactions could be related to pursuits for a potential food source in permanently populated places such as settlements and single houses within the forests used all-year-round (Gibeau et al. 2002, Jerina et al. 2012, Martin et al. 2010, Mohorović et al. 2017, Elfström et al. 2014, Nellemann et al. 2007). Other telemetry studies investigate the effects of supplementary feeding stations (Krofel et al. 2017, Selva et al. 2017) or popular touristic places / seasonal recreational resorts have on bear behaviour (Rode et al. 2006). Most of these sources deal with certain aspects of bear behaviour but do not relate it to the capture effect.

We conducted analyses based on data from a small-sized sample of nine GPS-collared brown bears to identify key issues of the potential link between the capture as an event in the bears' lives and the following interaction with areas that might be associated with a risk of capture. We tested the hypothesis that, after capture and handling, the collared bears avoid places posing a risk of recapture. To confirm or reject this hypothesis and account for the possible habituation effect, the individuals were divided into two groups: Group A – captured on a feeding station (with presumed habituation to human-provided food) and Group B – captured on another type of site (unknown habituation). In both groups, three major effects were analysed, aiming specific objectives:

1. Capture site effect, testing if bears tend to remember the capture location and avoid as a threat of immediate risk of recapturing. *Objectives:* 1. Determine if the bears returned to the location where they were caught and, if they did, in how many days. 2. Determine the distance bears kept from the capturing site.

2. Feeding station effect, testing if the bears are avoiding the supplementary (artificial) feeding stations as a *potential* threat for recapture. *Objectives:* 1. Determine if the bears perceived the supplementary feeding stations (which humans visit to provide food) as a threat for recapture, e.g. if bears visited feeding stations after capture. 2. Determine the distance the bears kept from the supplementary feeding stations. 3. Determine the possible cumulative effect with the proximity of the capture site.

The *capture site effect* objectives are set to identify the animals' memory and response to immediate / present risk (the capture event). The *feeding stations effect* objectives are related to perceived risk, which the humans might represent.

Materials and Methods

Study area

Our study falls within the boundaries of the Central Balkan National Park, its buffer zone and the grounds of several State Hunting Enterprises (SHE)

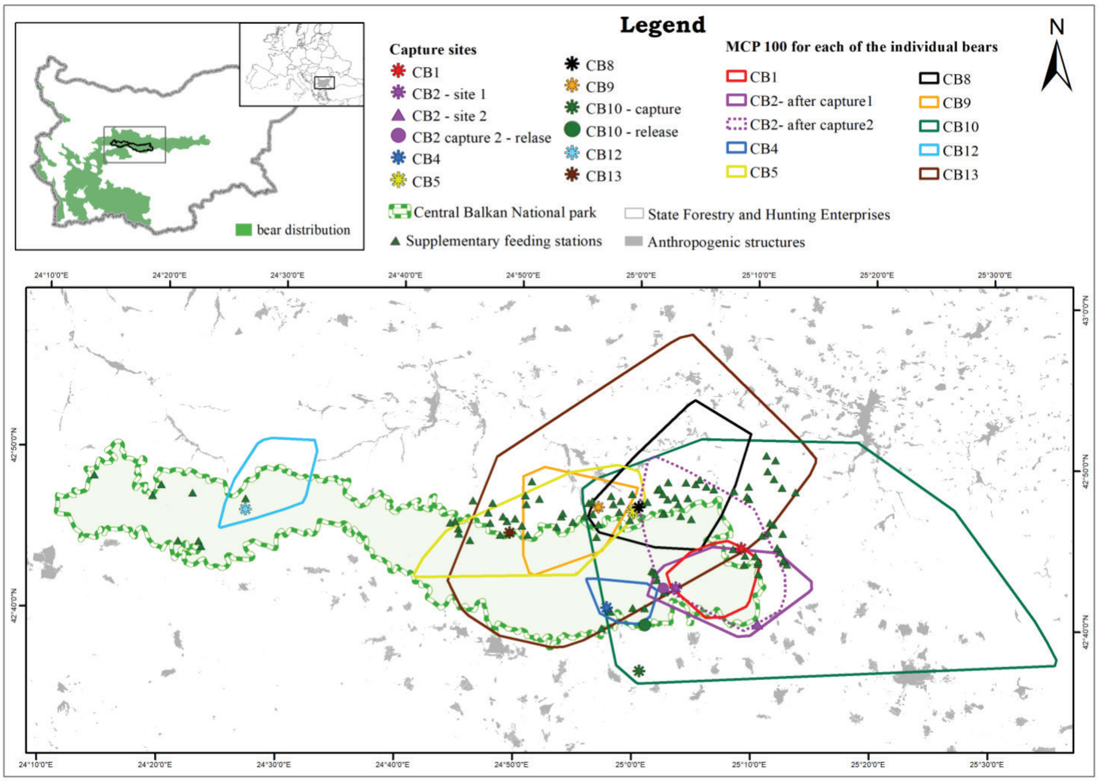

Fig. 1. Study area with capture sites, supplementary feeding stations and minimum convex polygon (MCP100) for the individual bears' telemetry locations in the study area.

and State Forestry Enterprises (SFE) (Fig. 1). The State Hunting Enterprises *per se* are forestry enterprises (for management of forests and timber production) but with additional sets of activities, such as intensive game management that includes supplementary feeding.

The Central Balkan National Park (NP) spans on an area of 716.7 km^2, with the highest peak reaching 2376 m.a.s.l. More than 56% of the park is covered with forests, predominantly beech (*Fagus sylvatica*), while the rest of the territory consists of meadows and pastures with abundant berries and junipers (CB Administration 2019). This NP protects one of the most extensive and compact, relatively low-urbanised beech forest complexes on the Balkan Peninsula, with an average age of the trees being 133 years. The Central Balkan NP and its surroundings are covered by four forest belts (Asenov 2006): 1. The xero-thermophilic oak (*Quercus* sp.) belt; 2. The oak and hornbeam (*Carpinus* sp.) belt; 3. The beech belt; 4. The coniferous belt. The territory of the national park is divided into areas under full protection (such as strict reserves, where all anthropogenic activities are forbidden) and areas where some human activities are allowed.

The study area is located within the Central Balkan segment of the Eastern Balkan population of the brown bear in Bulgaria (Linnell et al. 2008, Kaczensky et al. 2013). The population size in the area is reported to be around 100 individuals (MoEW 2008), thus the sample size of collared bears in our study is representative for this population segment.

The study area is unevenly populated, with an average human density of c. 58.7 people/km^2 (range: 14.02–117.54). Due to the national park's regulations, no permanent settlements are allowed on its territory. However, there are 30 villages in nine municipalities in proximity and around the park's border. The national park's regulations provide ground for cattle and sheep pasture, where goats are not allowed.

One hundred and six supplementary feeding stations (Fig. 1) for ungulates (red deer *Cervus elaphus* L., 1758, wild boar *Sus scrofa* L., 1758 and roe deer *Capreolus capreolus* (L., 1758)) are registered (if the feeding stations are still in use). These stations are mainly in the hunting grounds of the State Hunting and Forestry Enterprises, as required by the Regulation of Hunting and Game Conservation act (MAFF 2001). Twenty-eight of them are in the national park providing food mostly in the winter or on irregular intervals during the other seasons. The food provided on all the feeding stations is maize (*Zea mays*). Bears are generally attracted by this

Table 1. Details for the captured and collared bears used in this study: ID, type of capture location, group according to capture: Group A (caught at feeding stations) and Group B (caught at other sites), sex, age at capture (estimated by the teeth status), tracking period, the number of GPS fixes collected, numbers of GPS fixes resampled at 12 hour period, MCP100, km^2. The ID of the individuals follows the capture order.

Bear ID	Type of capture location	Group according to capture	Sex	Age, years	Tracking		Total number of fixes	Number of resampled fixes (12 h)	MCP 100 (km^2)
					Period	Days			
CB1/ Chara	Feeding station	Group **A**	F	~3	22.9.2007–29.7.2008	310	3194	407	65.60
CB2-s1/ Rusi	On animal trail	Group **B**	M	~2.5	3.11.2009–29.9.2010	330	1788	362	119.3
CB2-s2/ Rusi*/**	Poacher's snare	Group **B**	M	~3.5	29.9.2010–20.11.2010	52	742	104	201.15
CB4/ Mitko	On animal trail	Group **B**	M	~4–5	25.11.2014–16.6.2015	203	616	157	30.7
CB5/Ivanka***	Feeding station	Group **A**	F/cub	~1.5	8.6.2016–29.4.2017	325	3199	357	206.3
CB8/ Andrey	Feeding station	Group **A**	M	~5	30.10.2016–2.8.2018	641	2712	806	192.63
CB9/ Plamen***	Feeding station	Group **A**	M/cub	~2	2.11.2016–1.9.2017	303	1131	375	112.76
CB10/ Jimmy**	Poacher's snare	Group **B**	M	~2	8.6.2017–20.5.2018	346	3345	623	1157.55
CB12/ Boriana	On animal trail	Group **B**	F	~4–5	7.3.2018–19.10.2018	226	2183	407	108.27
CB13/ Spiridon	Feeding station	Group **A**	M	~6–7	12.12.2017–20.12.2018	373	8775	582	857.88

* Recapture (poacher's snare)
** Released in a different from the capture location
*** Cub considered in the females' group, representing mother's behaviour

food of high nutritional value as Gunchev (1989) has confirmed a high percentage of corn intake by the species for that area. Additionally, bears were frequently registered by camera traps at supplemental feeding stations. On the hunting grounds, the food is provided more intensively, once per every 1–2 days in winter and spring and at least once per week in the other seasons. During our study, 73.6% of these feeding stations were providing food regularly and 26.4% were seasonal. Because of the variability of feeding stations management (differences in the frequency of feeding was found, even within the same stations) for this study, we assumed that all the feeding stations were attractants for the bears *per se*. All of the feeding stations were visited for food or simply checked by bears, regardless of the intensity and type of feeding. None of the stations was providing enough food to sate one individual bear, especially with the competition of wild boars and red deer.

Capture and handling of bears

The capture sites and capture season were chosen based on bears' presence, according to information from the NP and SFE / SHE staff and camera trap data, recording the frequency of bear visits to the potential capture site. Two or three standard Aldrich snares (Aldrich Snare Co., Washington) were used for capturing per trap-site. The snares were placed near a tree with a bag hanging on it, containing a mixed bait of corn and honey. The trap placement was following the guidelines of Jonkel (1993). MMS camera-traps (Ltl Acorn / model LTL5210-MG) were used as a bear capture alert system during the night, to minimise the bear stay in the trap to less than two hours.

During the study period (2007–2018), in overall 25 trapping nights, we captured 13 bears, nine of which were used in the current analyses (Table 1). The rest were either not collared because of the small body size or the collars defected a few days after the release. Two of the collared bears (CB5, CB9) were two-year-old cubs, led by their mothers, which were also present at the capture site. Both had been with their mothers until the next spring (between six and eleven months); that is why we consider both in the group of females since they represented their mother's territory. Five bears were captured on feeding stations, three were captured on animal trails, one (CB10) was rescued from a poacher's snare (Table 1). One of the bears (CB2), previously captured on a trail, was later rescued from a poacher's snare. The two individuals (CB2 and CB10) were later released away from the poaching site, within the boundary of the national park in an optimal habitat with good visibility cover: CB2 in about 12 km straight line distance from capture, CB10 in about 5 km from the capture site. Both bears were transported and released under the effect of the first immobilisation.

All bears were captured during the night. The capture site locations and the minimum convex polygon (MCP100) for each bear based on all telemetry locations are presented on Fig. 1.

For each capture, the bears were immobilised via Teledart CO_2 injection gun with a mixture of Tiletamine/Zolazepam (Zoletil Virbac 50 / 100: 2.5–3 mg/kg) and medetomidine hydrochloride (Domitor 1mg/ml: 0.05 mg/kg). The animals were able to see the approaching human during the sedation process. The time to full sedation varied in the range of 7 to 54 min, while the time to full recovery (bear moving away) varied between 49 min to around 7 hours, depending on the body weight, fat deposits and age of the animal. Due to the lack of reversal agent for Tiletamine and the high doses of Tiletamine-Zolazepam mix, preventing the use of antagonists, no reversal agents were used to aid the recovery of the animals (Arnemo & Fahlman 2007). All manipulations with the bears lasted less than 30 minutes, with their eyes covered during the procedure. The animals were weighed and measured, and the status of the teeth was recorded for assessment of the age.

Two different types of GPS collars were used in this study: Vectronic (Vectronic GPS pro lite, collar weight > 810 g, Vectronic Aerospace GmbH, Germany) and Followit (Tellus GPS Medium Plus, collar weight > 980 g, Followit, Lindesberg AB, Sweden), equipped with GSM module for data transfer. All collars were also equipped with VHF transmitters, UHF-communication to download the data directly, an activity sensor and drop-off system.

After the handling procedure, the animals were left on undisturbed places and were monitored from a distance until their full awakening and moving away from the capture site.

Data collection

The collars were initially set to record the locations at a varying time interval, ranging from two to 12 hours, depending on the season: every 2 hours during spring, summer and autumn and every 12 hours during winter (power save mode). This called upon the need for sub-sampling to equal time frame to be able to analyse and compare the step length (the Euclidean distance between each location in sense of animal displacement in space) across time and individuals throughout the whole study period. Twelve hours between each location fix (one night location at 00:00 h and one day location at 12:00 h) were chosen (Table 1) to compromise between the shortest step length possible, the time overlap of GPS fixes from each of the collars and the continuousness (no fixes missing) in the data flow. This resampled data was used for analyses of the distances the individuals keep from capture sites and feeding stations. The full set of data was used to identify the visits (explained herein below) to capture sites, feeding stations and anthropogenic structures.

Spatial analyses

The feeding station's locations (supplementary feeding for ungulates) were mapped with a GPS device at the centroid of the feeding ground (with an average area of approximately 30x30 m). For each of the individuals, a density of feeding stations per 1 km^2 was calculated as the number of stations present in the animal MPC100 polygon, divided by the area of the MCP.

All spatial analyses were conducted with ArcGis Desktop 10.2.2 – ArcMap (ESRI). The resampling of the locations to 12-hour interval and the calculation of individual displacement (step length) for this timeframe were done with ArcMET 10.2.2.v3 extension for ArcGIS Desktop (Wall 2014). The distance and visits to capture sites and feeding stations were calculated with *Near* function of ArcMap. A 50 days mobility data after the capture event was analysed for the two sub-adult male individuals with capture and release in different locations – CB2 (second capture) and CB10. This was done to test which location was perceived as more threatening: capture or release. To test for avoidance or possible habituation, the pool of all fixes within the range of 0 to 500 m distance from the capture sites and feeding stations (calculated as a distance to the centroid) were analysed. They were divided into three distance classes: *visit* (0-30 m), *approach* (31-100 m) and *proximity* (101-500 m). The 30 m values were taken from the average position error under forest canopy for the two types of GPS collars used, with the error being tested in the field. The 100 and 500 m ranges were the most common measure the local people in the nearby settlements use to define bears "approaching" (100 m) and "proximity" (within the limits of 100-500 m.)

For the spatial analyses of the capture site effect, the location data for the first 48 hours were removed to account for the full recovery time after sedation (Cattet et al. 2008) before the animal completely moves away after capture and to avoid double counting of the animal presence at a feeding station when it was also a capture site.

Statistical analyses

We tested for individual, gender-specific and group differences in the distances the animal keep from the capture sites as well as feeding stations, using the non-parametric Mann–Whitney and Kruskal–Wallis statistics. In the individual and groups' statistical comparisons, where after testing with Shapiro-Wilks test, a deviation from normality for the distances from the capture sites and feeding stations in both groups (A and B) was present, the median was used instead of average. Exact binomial test of goodness-of-fit was used to compare the difference in the proportion (1:1) in the number of visits to captures sites and feeding stations between the two groups, as well as the animals' presence in the respective proximity and approach zones. For the statistical analyses, these visits or presence were expressed as the *relative frequencies* F_v (visit), F_a (approach), F_p (proximity), representing proportions of days spent in visit/presence for each individual towards the overall tracking days. The differences were tested with two-tailed probabilities at 0.05 significance, within the 95.0% confidence level. All statistical analyses and plots were done with Statgraphics Centurion 18.1.11 (Statgraphics Technologies, Inc.). The variation of Euclidean distances from the capture sites, and feeding stations were plotted with violin graphs with cosine function and interval width (h) at 10 %.

Results

Capture site effect

Capture site visits. All bears kept the capture sites as part of their home ranges. Three individuals, all males returned to the capture site – two of the Group A (capture site also feeding station) and one of the Group B. The capture sites of the Group B individuals to the nearest feeding station were at a distance from 1.3 to 6.6 km, except for CB4 (82 m). The individuals of the Group A (caught at feeding stations) exhibited more pronounced, yet not significantly different relative frequencies of visits to the capture sites (Exact test of goodness-of-fit (ETGF) on proportions of medians, p>0.05) than those of the Group B (Table 2). No significant difference was found in the relative frequencies of visits to the proximity and the approach zones between the two groups (ETGF, p>0.05). Eight of all nine capture site visits were between 1:00 am and 7:00 am. Most of the returns to the capture sites (n = 6) for the Group A were in the spring (April-May).

Table 2. Visits, approach and proximity to the capture sites (presented as number of days and their respective relative frequencies F_v, F_a, F_p) and days to the first visit after capture for the individual bears and groups: Group A (caught at feeding stations) and Group B (caught at other sites), with Exact binomial test comparison on medians between the two groups.

Group	Bear ID	Visit (0–30 m)	F_v	Approach (31–100 m)	F_a	Proximity (101–500 m)	F_p	Days to first visit after capture
A	CB1	0	0.000	0	0.000	2	0.006	-
	CB5	0	0.000	0	0.000	0	0.000	-
	CB8	6	0.009	3	0.005	20	0.031	146
	CB9	0	0.000	0	0.000	1	0.003	-
	CB13	2	0.005	1	0.003	3	0.008	142
B	CB2-s1	0	0.000	0	0.000	1	0.003	-
	CB2-s2	0	0.000	0	0.000	0	0.000	-
	CB4	0	0.000	0	0.000	6	0.030	-
	CB10	1	0.003	2	0.006	7	0.020	70
	CB12	0	0.000	1	0.004	41	0.181	-
Exact binomial test (Group A vs. B)			p>0.05		p>0.05		p>0.05	

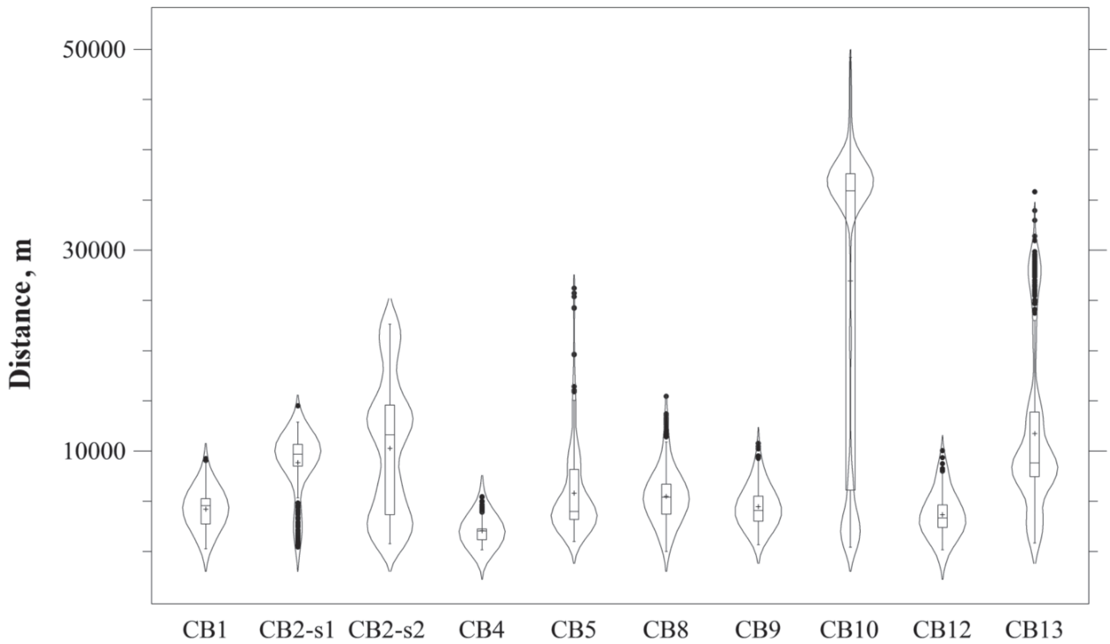

Fig. 2. Distance to capture site for all individuals. The two captures of CB2 are marked as CB2-s1 and CB2-s2 according to the capture order. Horizontal line = median value, plus sign = average, Box = interquartile range, the vertical width = probability density of the data for each individual plotted with nonparametric density estimator, points = outliers.

Capture site distance. The GPS-collared brown bears in our study displayed statistically significant differences in the distance which they keep from their capture sites (Kruskal–Wallis test, H = 1413.12, df = 9, $p < 0.005$). Additionally, the interquartile range of these distances (Fig. 2) showed a great variability (range 1078–30395 m) and with numerous outliers, depending on the sex and age of the individuals. Most of the individuals (n = 6) exhibited unimodal density distribution of the distance they kept from the capture site, at they tend to keep more or less stable "safe" straight line distance of at minimum 2 km. Two male individuals, CB10 and CB13 exhibited the highest displacement distance related to the capture site.

For both animals translocated after capture (CB2 after second capture and CB10), the release sites as well as the capture sites continued to be present within the home range. There was a statistically significant difference between the median distance to the capture sites for both captures of the CB2 individual – CB2-s1 and CB2-s2 (Fig. 2) (Mann–Whitney test, W = 21353.5, $p < 0.005$). Yet, no statistically significant difference was found between the median distances CB2 kept to both capture and release sites after the second capture (Mann–Whitney test, W = 5678.0, $p > 0.005$). Generally, this individual kept a larger distance from the second capture site (Fig. 3). Most of the CB2 locations showed a retreating pattern with a unimodal distribution of the distances from the release site, peaking at 11 km. For CB10, there was a statistically significant difference between the median distances it kept from the capture and release sites (Mann–Whitney test, W = 8705.5, $p < 0.005$), again with a more prominent median distance from the release site (5 km) than from the capture site (1.6 km). This difference in the distances from the capture and release site was preserved for the whole period of our study.

The median distances which males and females kept to the capture sites (Fig. 4A) were not significantly different (Mann–Whitney test W = 4.0, $p > 0.05$). The same was found for the comparison between the Groups A and B (Fig.4B, Mann–Whitney test W = 15.0, $p > 0.05$).

Feeding stations effect

Feeding stations visits. The CB1 (young female) and CB9 (male cub with its mother) individuals, despite being caught on a feeding station, have never visited such station again. On the contrary, the other cub CB5 with its mother of the same group (A) was registered earliest on a feeding station (four days after capture), but such a visit was never repeated for the whole period of tracking. Without this case, the days to the first visit on a feeding station after capture varied between 22 and 146 (Table 3).

Generally, the Groups A (caught at feeding stations) showed pronounced numbers of visits, although

Table 3. Visits, approach and proximity to the feeding stations (presented as number of days and their respective relative frequencies F_v, F_a, F_p) and days to the first visit after capture for the individual bears and groups: Group A (caught at feeding stations) and Group B (caught at other sites), with Exact binomial test comparison on medians between the two groups

Group	Bear ID	Density of FS in HR per 1 km²	Visit (0–30 m)	F_v	Approach (31–100 m)	F_a	Proximity (101–500 m)	F_p	Days to first visit after capture
A	CB1	0.09	0	0.000	3	0.010	41	0.132	-
	CB5	0.22	1	0.003	8	0.025	76	0.234	4
	CB8	0.21	12	0.019	62	0.097	177	0.276	146
	CB9	0.18	0	0.000	2	0.007	43	0.142	-
	CB13	0.05	13	0.035	41	0.110	74	0.198	94
B	CB2-s1	0.1	0	0.000	0	0.000	21	0.064	-
	CB2-s2	0.15	2	0.038	5	0.096	14	0.269	22
	CB4	0.12	0	0.000	0	0.000	17	0.084	-
	CB10	0.04	0	0.000	1	0.003	13	0.038	-
	CB12	0.02	0	0.000	1	0.004	11	0.049	-
Exact binomial test (Group A vs. B)		p>0.05		p>0.05		p>0.05		p>0.05	

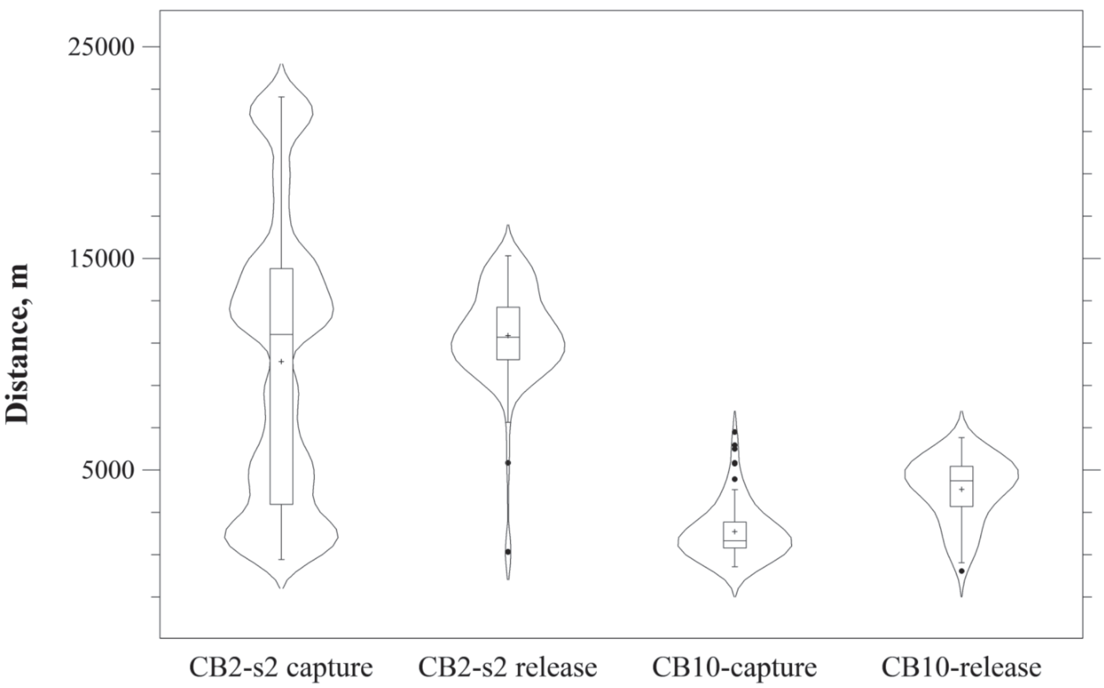

Fig. 3. Distance to capture and release site for the individuals CB2 and CB10 for the first 50 days after release. Box = interquartile range, horizontal line = median value, plus sign = average, the vertical width = probability density of the data for each individual plotted with nonparametric density estimator, points = outliers.

relative frequencies of visits to the feeding stations were not significantly different (ETGF, p>0.05) compared to the Group B (60% vs. 20% of all individuals in the group, see Table 3). Also, no statistically significant difference was found in the density of feeding stations per 1 km² in the home ranges of both groups. Additionally, no correlation was found between the density of feeding stations and relative frequencies of visits in the Group A (Pearson correlation, p > 0.05) and the Group B (Spearman correlation, p > 0.05). In the Group A, CB8 and CB13 male individuals showed repeated visits on feeding stations, including the same stations on which they were caught (CB8 n = 6; CB13 n = 2). In the younger CB8, 50% of feed-

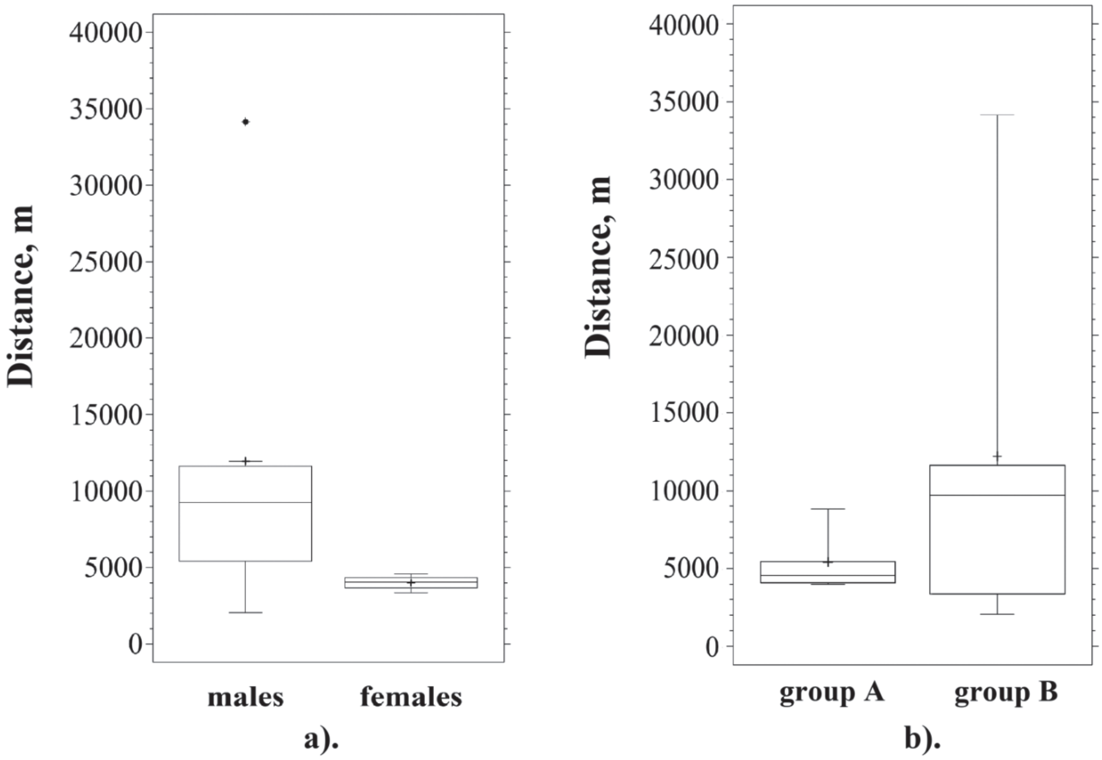

Fig. 4. Comparison of the distance to capture sites in males and females (a) and Group A and Group B (b). Box = interquartile range, horizontal line = median, plus sign = average, lower whiskers = min. value, upper whiskers = max. value, filled points with plus sign – far out outliers (more than three interquartile ranges).

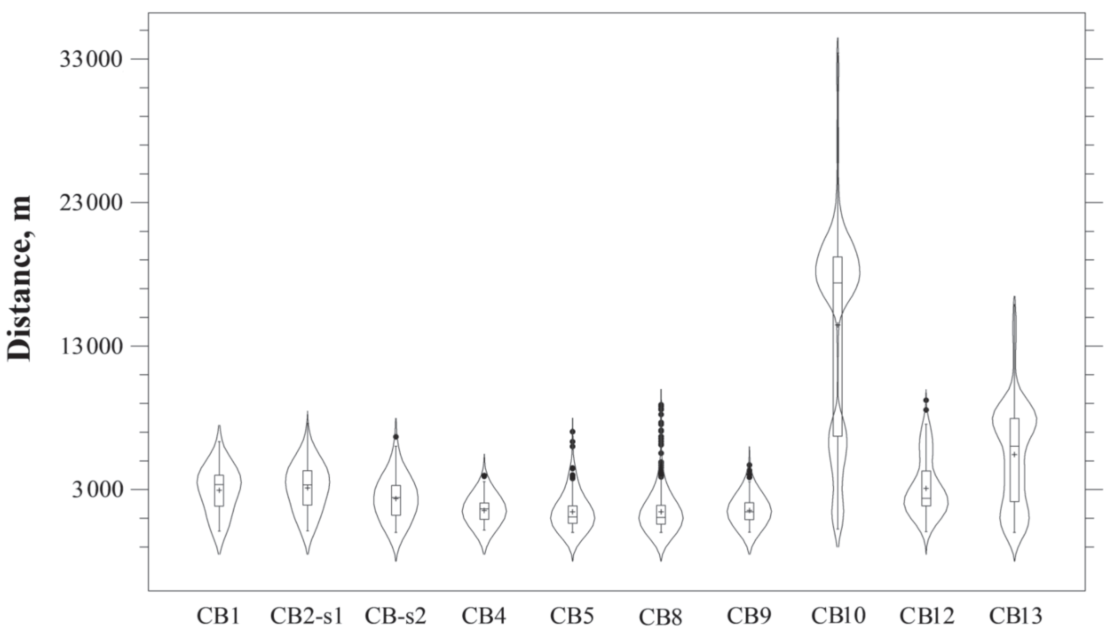

Fig. 5. Distance from feeding stations for all tracked individuals. Box = interquartile range, horizontal line = median value, plus sign = average, the vertical width = probability density of the data for each individual plotted with nonparametric density estimator, points = outliers.

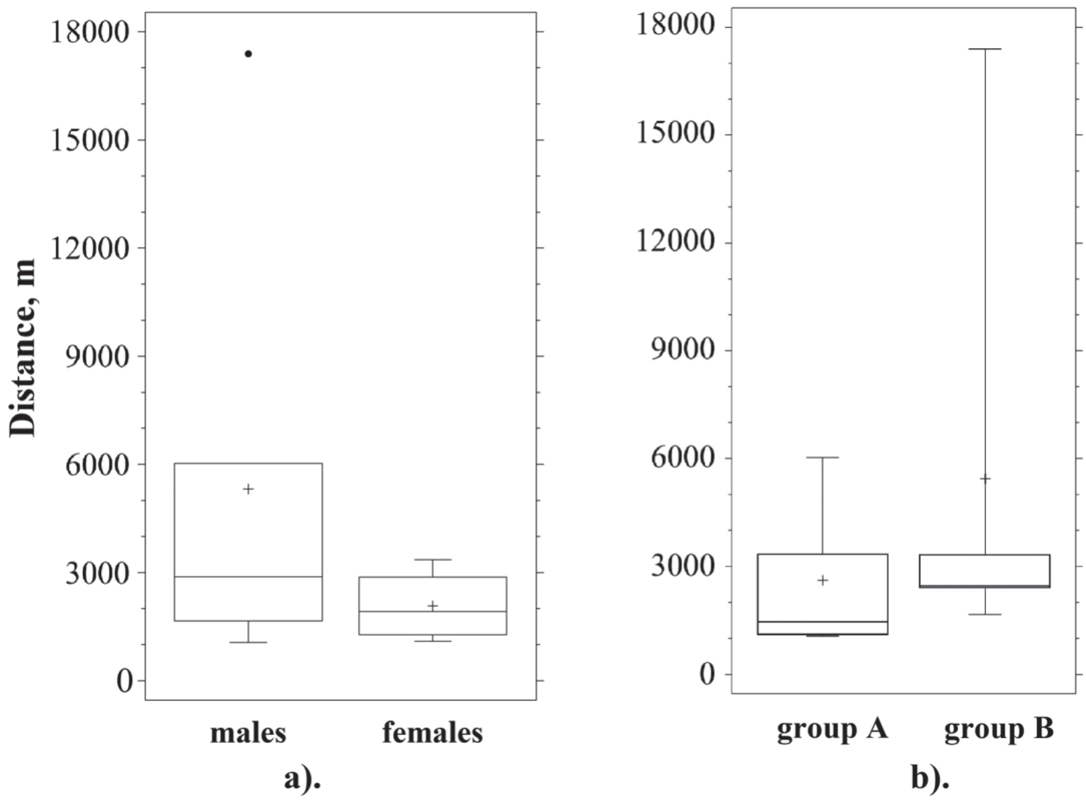

Fig. 6. Comparison of the distance **to** feeding stations in males and females (a) and Group A (captured on a feeding station) and Group B (captured on other sites) (b). Box = interquartile range, horizontal line = median, diamond = average, lower whiskers = min. value, upper whiskers = max. value

ing stations visits were at the location where it was caught, although it had lower relative frequencies of visit than the older CB13 individual (0.019 vs 0.035) who also appeared on a feeding station earlier (around three months after capture). In the Group B, despite that CB4 was caught very close to a feeding station (around 80 m), it was never recorded on one, during the tracking period. An interesting observation is that before the recapture, CB2 (Group B) did not visit any feeding stations but, after the recapture, the individual was recorded on a feeding station twice, as the first capture location was closer to feeding stations than the second (1.3 vs 5.8 km).

No statistically significant difference was found between the two groups in the relative frequencies of locations in the proximity and approach zone (ETGF, $p > 0.05$). The individuals of the Group A tend to stay longer in these zones than the individuals from Group B.

Feeding stations distance. In the median distances to feeding stations, a statistically significant difference was found between all the tracked individuals (Kruskal–Wallis test, $H = 1413.12$, $df = 9$, $p < 0.005$). Using the Bonferroni procedure, no statistically significant difference was found between the median distances to feeding stations after the first and second capture of CB2 individual. Most of the tracked individuals kept a close distance of no more than 3 km to feeding stations (Fig. 5). The comparison of median distances to feeding stations between males and females (Mann–Whitney test, $W = 8.0$, $p > 0.05$) and between the Group A and the Group B (Mann–Whitney test, $W = 17.0$, $p > 0.05$) did not show statistically significant differences (Fig. 6). Yet, the Group A stayed closer to the artificial feeding sites.

Discussion

First, we would like to acknowledge the small sample size of the collared individuals (9 bears, 10 cases) in our study. Although presented with reasonably enough duration of tracking (>50 days) and mobility data (>500 locations per animal) we recognise that it cannot be used for universal conclusions of the species behavioural traits. However, the outcome is representable for the population in the area, given the overall size of it (around 100). Despite the disadvantages of the small sample size, the large number of fixes per individual (Hebblewhite & Haydon 2010) provided valuable insights into ‘after capture’ level of avoidance of risky (perceived or real) areas of the tracked bears from this poorly studied population.

Small sample size in sense of individuals is still an issue of many related GPS-telemetry studies (Selva et. al. 2017), provided the very high costs of GPS collars and the challenge bear capture represent.

The effect of the capture in brown bears is poorly studied, with only the movement rates being at focus (Cattet et al. 2008). The avoidance behaviour after capture, related to humans is not studied at all. It is generally believed and often implied that, after capture, bears tend to avoid people or the areas where the likelihood of encountering humans increase significantly (Gillin et al. 1994). Bears in Sweden temporary altered their movement patterns after encounter with or approach by humans (Ordiz et al. 2019). The capture is expected to have even more prominent effect. This is often explained with the so-called "negative conditioning (reinforcement)", proposed by B. F. Skinner in his theory of operant conditioning (Skinner 1963). In the sense of the "Negative / Reinforcement theory", the capture is perceived as a punishment – the physical and psychological health of the animal is challenged. Cattet et al. (2008) has shown that during the capture, the time spent in the trap was the extremely stressful for the animals and resulted in negative conditioning. Trapping the animal with a snare is a painful experience and not often but might results in injuries of the limbs, which was the case in one of our individuals (CB2 – second capture in a poacher's snare).

Thus, capture was expected to contribute to avoidance behaviour of places that might result in a negative outcome – in the case of bears, avoidance of all places with an immediate, perceived or present risk of capture. In our study the avoidance of the immediate risk, which the animals experienced at capture sites was stronger (in 70% of all cases). This could be interpreted at least in two ways (Travaini et al. 1993): 1. Being a stressful event, the capture often forces the animals to change their home range, so the capture site was left at the edge or outside it. Similar behaviour was confirmed in other species like Eurasian lynx (*Lynx lynx*) and roe deer (*Capreolus capreolus*) (Moa et al. 2001, Morellet et al. 2009). In red foxes (*Vulpes vulpes*), stressful capture experience leads to avoidance of the capture patch (Travaini et al. 1993). This was coherent with our study, too, as the capture sites were closer or at the edge of the home range border (Fig. 1). 2. Another possible explanation of the strong avoidance may be that the capture occurred outside the normal home range of the animals, where animals show more investigative behaviour. In our study, the first explanation seemed to be supported better by our data, as returns to the capture sites are still noted. However, due to the small sample size, more data are needed to accept or reject this conclusion.

Avoidance of feeding stations was less than that of the capture sites (in 60% of all cases). Apart from the capture effect, a possible explanation of the high level feeding station avoidance could be the pressure from the despotic behaviour of dominant conspecifics (Elfström et al. 2014).

However, our results showed that despite the capture event, bears did not entirely avoid the capture sites or the feeding stations. For example, after the second capture of CB2 in poacher's snare near anthropogenic structures, this individual not only started to visit feeding stations (probably due to his advancement in age and body size, making him more competitive) but has also continued to visit anthropogenic structures. Yet, some negative conditioning could be observed in few individuals as the female CB1 and the male CB9, sub-adults at capture (2-3 years old) – after being caught at a feeding station, they never visited one. No visit to anthropogenic structure was recorded in CB9 either, while CB1 even avoided inclusion of such structure in its home range polygon.

Yet, bears had very diverse response to the capture effect in respect of the distance they kept from the capture sites and feeding stations. The brown bear is well-known for its high intelligence and individuality, as experience and sex (especially in females with cubs) play a major role in behavioural responses. In roe deer (Morellet et al. 2009), the young or males were more susceptible to stress-related behaviour strongly avoiding capture sites. In comparison, although there was not a significant difference in our males' and females' responses to the immediate risk (capture site) in sense of distance from it, only males (n = 3) has visited the capture site again. Two of the Group A bears visiting their captures sites (5 and 6-7 years old) were mainly driven by the available food source (capture site was also a feeding station). For the younger male, the food attractiveness seemed to overcome the capture stress-related effect over time – 50% of the feeding stations visits coincided with the capture site. Both bears returned to these sites in the spring driven by the shortage of food. Yet, the Group A bears needed more time to overcome this stress and restart visiting feeding stations than the CB10 individual from Group B.

While males in our study were heterogeneous group in their avoidance behaviour, females (with exception for the cub CB5 with its mother) were showing strong avoidance to the two disturbance factors (capture sites and feeding stations). The deviation from this avoidance behaviour in CB5 was expressed both in: the earliest (from all the studied individuals) visit to a feeding station (four days after capture), despite that the cub was caught in a feeding station. Such lack of fear in a female with cub is usually typical to either bears habituated to utilize food provided by human presence or is related to the so called "safety search" behaviour (Elfström et al. 2014) of female bears with cubs/yearlings against infanticide by adult males or pressure from the despotic behaviour of dominant conspecifics.

Experience might be also shaping the avoidance behaviour in our study. The sub-adult male CB10 (Group B) has overcome the stress from capture twice as early (in respect of capture site visit – 70 days) than the other two, older males of the Group A (142 and 146 days, respectively). The CB10 individual had the highest mobility of all individuals, yet Hertel et al. (2019) stated that individuals that are more mobile were not necessarily bolder. Thus, the difference may be due not only to the experience but also to the cumulative effect for the Group A males of both capture site and feeding station coincidence. The other two sub-adults, CB1 (female) and CB9 (male), did not visit any feeding stations (or anthropogenic structures) and CB1 never even approached them. Lack of visits to feeding stations in an opportunistic species as the bear is often due to a "landscape of fear" formed either from fear from dominant conspecifics or from humans (Domevscik et al. 2018).

Our results about the level of avoidance could be explained by two factors: 1. Presence of two types of memories related to bears' movement and navigation in space (Fagan et al., 2013): *spatial memory* related to the configuration of objects and *attribute memory* connecting the attributes of these objects in space (like sound, smell). 2. Compromise between the attractiveness of food sources and risk involved for obtain it (competition with conspecifics, other species like the wild boar and fear of humans). The history of previous captures of habituated bears to food provided by humans (intentionally or unintentionally) impedes the recapture due to trap avoidance (Leigh & Chamberlain 2007) as sometimes this task is impossible. This implies that the bears are capable of memorizing not only the negative experiences associated with capture but also triggers their spatial and attribute memory in the avoidance process.

In case when capture and release sites were different (as in the CB2's second release and in CB10 relocation after capture), the memory of negative experience of the capture itself could be transferred to the release site, especially when (as in our case) no reversal agents were used to aid the quick recovery of the animals. Acknowledging the small sample size and the need for a bigger sample for a more confident statement, we assume that there was high probability evidence that the release site was more stressful in the memory of the animals than the capture site. It might be true for two reasons: not only because longer awaking process forced the bears to spend more time immobilised in proximity to humans (accelerating the stress) but also because the animals were forcedly placed immobilised in an area already inhabited by other bears. Another factor with a cumulative effect might be the time spent in the trap before anaesthesia, which was adding to the overall stress. This resulted in similar behaviour in both CB2 and CB10 – they returned in the area where they were captured (apparently part of their original home range), which they perceive as "safer" than the one of the release.

The bears are well-known for adapting quickly to their environment. The strength of the stimuli and stress during capture as well as animal individuality play a vital role in forming a variable response to the risk the capture site represent. Whether the animal will adapt to the presence of risk (perceived or present) by only temporary avoiding these areas or permanently avoiding them, depends very much on numerous factors, which are currently difficult to measure due to the lack of enough data collected. Our study confirms (as other studies do, see Majić Skrbinšek & Krofel 2013) that the capture event has a significant impact on the animal behaviour and can be efficient tool (at least in short term) for managing unwanted bear behaviour. This should be taken into consideration when capture and translocation of problem bears (caught near a food source) is planned as part of management interventions, with the intent of creating negative conditioning.

Conclusion

The hypothesis that the collared bears avoid places posing a risk of recapture is confirmed but no strong support has been found that this is a robust behavioural trait. The avoidance of the capture site effect has been found to be the unambiguously strongest. No definite conclusions can be drawn on the avoidance of feeding stations due to the capture, as this avoidance could be a result of despotic behaviour of dominant conspecifics. Further research on relation to seasonality could be beneficial and also a bigger sample size of bears to test these hypotheses further, in the sense of cross-country/cross-population comparison and to allow drawing some general conclusions for the species itself.

Acknowledgements: We would like to thank the Central Balkan National Park Directorate (Nikolay Staikov and Anton Stanchev) and "Rusalka" State Hunting Enterprise (Vasil

Shkembov) for the logistical support and assistance in collecting the necessary information. We also thank Alexander Dutsov and Kostadin Valchev (Balkani Wildlife Society) for their contribution and involvement in the fieldwork.

Funding: This work was partially supported by the Bulgarian Ministry of Education and Science under the National Research Program "Young scientists and postdoctoral students" approved by DCM # 577 / 17.08.2018 and by the State Enterprise for Management of Environmental Protection Activities (PUDOOS).

References

Arnemo J. & Fahlman Å. (Eds.) 2007. Biomedical Protocols for Free-ranging Brown Bears, Gray Wolves, Wolverines and Lynx. Norwegian School of Veterinary Science, Tromsø, Norway.

Asenov A. 2006. Biogeography of Bulgaria [in Bulgarian]. Sofia: Sofia University St. Kliment Ohridski Press, 543 p.

Brivio F., Grignolio S., Sica N., Cerise S. & Bassano B. 2015. Assessing the impact of capture on wild animals: The case study of chemical immobilisation on Alpine ibex. PLoS One 10: 1–18. https://doi.org/10.1371/journal.pone.0130957.

Cattet M., Boulanger J., Stenhouse G., Powell R.A. & Reynolds-Hogland M.J. 2008. An Evaluation of Long-Term Capture Effects in Ursids: Implications for Wildlife Welfare and Research. Journal of Mammalogy 89: 973–990. https://doi.org/10.1644/08-mamm-a-095.1

Cagnacci F., Boitani L., Powell R.A. & Boyce M.S. 2010. Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society. Series B: Biological Sciences 365(1550): 2157e2162. https://doi.org/10.1098/rstb.2010.0107.

CB Administration 2019. Central Balkan National Park Web site [WWW Document]. Gen. info. URL https://visitcentral-balkan.net/protected-areas/flora/forests/information-14-2.html (accessed 5.31.19).

Chapron G., Kaczensky P., Linnell J.D.C., von Arx M., Huber D., Andren H., Lopez-Bao J. V., Adamec M., Alvares F., Anders O., Bal iauskas L., Balys V., Bed P., Bego F., Blanco J.C., Breitenmoser U., Broseth H., Bufk, L., Bunikyte R., Ciucci P., Dutsov A., Engleder T., Fuxjager C., Groff C., Holmala K., Hoxha B., Iliopoulos Y., Ionescu O., Jeremi J., Jerina K., Kluth G., Knauer F., Kojola I., Kos I., Krofel M., Kubala J., Kunovac S., Kusak J., Kutal M., Liberg O., Maji A., Mannil P., Manz R., Marboutin E., Marucco F., Melovski D., Mersini K., Mertzanis Y., Mys ajek R.W., Nowak S., Odden J., Ozolins J., Palomero G., Paunovi M., Persson J., Poto nik H., Quenette P.-Y., Rauer G., Reinhardt I., Rigg,R., Ryser A., Salvatori V., Skrbin ek T., Stojanov A., Swenson J.E., Szemethy L., Trajce A., Tsingarska-Sedefcheva E., Vana M., Veeroja R., Wabakken P., Wolfl M., Wolfl S., Zimmermann F., Zlatanova D. & Boitani L. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346 (6216): 1517–1519. DOI: 10.1126/science.1257553.

Chi Da.K., Chester D. & Gilbert B.K. 1998. Effects of Capture Procedures on Black Bear Activity at an Alaskan Salmon Stream. Ursus 10: 563–569.

Domevscik M., Steyaert S.M.J.G., Swenson J.E., Lodberg-Holm H.K., Gelink H.W., Hertel A.G., Swenson J.E., Domevscik M., Steyaert S.M.J.G., Swenson J.E., Lodberg-Holm H.K., Gelink H.W. & Hertel A.G. 2018. A human-induced landscape of fear influences foraging behavior of brown bears. Basic and Applied Ecology 35: 18–27. https://doi.org/10.1016/j.baae.2018.12.001.

Elfström M., Davey M.L., Zedrosser A., Müller M., Barba M. De Støen O., Miquel C., Taberlet P., Hackländer K. & Swenson J.E. 2014. Do Scandinavian brown bears approach settlements to obtain high-quality food ? Biological Conservation 178: 128–135. https://doi.org/10.1016/j.biocon.2014.08.003.

Fagan W.F., Lewis M.A., Auger-Méthé M., Avgar T., Benhamou S., Breed G., Ladage L., Schlägel U.E., Tang W.W., Papastamatiou Y.P., Forester J. & Mueller T. 2013. Spatial memory and animal movement. Ecology Letters 16: 1316–1329. https://doi.org/10.1111/ele.12165

Flecknell P. 2002. Replacement, Reduction, Refinement. ALTEX – Alternatives to Animal Experimentation 19: 73–78.

Gibeau M.L., Clevenger A.P., Herrero S. & Wierzchowski J. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. Biological Conservation 103: 227–236. https://doi.org/10.1016/S0006-3207(01)00131-8.

Gillin C.M., Hammond F.M. & Peterson C.M. 1994. Evaluation of an Aversive Conditioning Technique Used on Female Grizzly Bears in the Yellowstone Ecosystem. International Conference of Bear Research Management 9: 503–512.

Gunchev R.R. 1989. Research on the numbers, the biology and the ecology of the brown bear (Ursus arctos L.) in Stara Planina mountain. Ph. D. Thesis. High Forestry – Technical Institute. Sofia, 128 p. [In Bulgarian].

Hebblewhite M. & Haydon D.T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society. B. Biological Sciences 365: 2303–2312. https://doi.org/10.1098/rstb.2010.0087.

Hertel A.G., Leclerc M., Warren D., Pelletier F., Zedrosser A. & Mueller T. 2019. Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. Animal Behaviour 147: 91–104. https://doi.org/10.1016/j.anbehav.2018.11.008.

Jerina K., Krofel M., Stergar M. & Videmšek U. 2012. Factors Affecting Brown Bear Habituation To Humans: a GPS Telemetry Study. University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Ljubljana.

Jonkel J.J. 1993. A manual for handling bears for managers and researchers. U.S. Fish and Wildlife Service, Montana.

Kaczensky P., Chapron G., von Arx M., Huber D., Andrén H., Linnell J., Adamec M., Álvares F., Anders O., Balciauskas L., Balys V., Bedo P., Bego F., Carlos Blanco J., Boitani L., Breitenmoser U., Brøseth H., Bufka L., Bunikyte R., Ciucci P., Dutsov A., Engleder T., Fuxjäger C., Groff C., Heltai M., Holmala K., Hoxha B., Iliopoulos Y., Ionescu O., Ivanov G., Jeremić J., Jerina K., Kojola I., Kos I., Krofel M., Kubala J., Kunovac S., Kusak J., Mannil P., Manz R., Marboutin E., Marucco F., Melovski D., Mersini K., Mertzanis Y., Mysłajek R.W., Nowak S., Odden J., Ozolins J., Palomero G., Paunovic M., Persson J., Potočnik H., Quenette P.-Y., Rauer G., Reinhardt I., Rigg R., Ryser A., Salvatori V., Skrbinšek-Majić A., Stojanov A., Swenson J., Trajçe A., Tzingarska-Sedefcheva E., Váňa M., Wölfl M., Wölfl S., Zimmermann F. & Zlatanova D., 2012. Status, management and distribution of large carnivores – bear, lynx, wolf & wolverine – in Europe. Part 1 (Europe summaries), European Commission Series. European Commission, contract N°070307/2012/629085/SER/B3.

Kaczensky P., Chapron G., von Arx M., Huber D., Andrén H., Linnell J., Adamec M., Álvares F., Anders O., Balciauskas L., Balys V., Bedo P., Bego F., Carlos Blanco J., Boitani L., Breitenmoser U., Brøseth H., Bufka L., Bunikyte R., Ciucci P., Dutsov A., Engleder T., Fuxjäger C., Groff C., Heltai M., Holmala K., Hoxha B., Iliopoulos Y., Ionescu O., Ivanov G., Jeremić J., Jerina K., Kojola I., Kos I., Krofel M., Kubala J., Kunovac S., Kusak J., Mannil P., Manz R., Marboutin E., Marucco F., Melovski D., Mersini K., Mertzanis Y., Mysłajek R.W., Nowak S., Odden J., Ozolins J., Palomero G., Paunovic M., Persson J., Potočnik H., Quenette P.-Y., Rauer G., Reinhardt I., Rigg R., Ryser A., Salvatori V., Skrbinšek-Majić A., Stojanov A., Swenson J., Trajçe A., Tzingarska-Sedefcheva E., Váňa M., Wölfl M., Wölfl S., Zimmermann F. & Zlatanova D. 2013. Status , management and distribution of large carnivores – bear, lynx, wolf & wolverine – in Europe. Part 2 (Country reports), European Commission. European Commission, contract N°070307/2012/629085/SER/B3.

Krofel M., Špacapan M. & Jerina K. 2017. Winter sleep with room service: denning behaviour of brown bears with access to anthropogenic food. Journal of Zoology 302: 8–14. https://doi.org/10.1111/jzo.12421.

LCIE 2007. Policy Support Statements of the Large Carnivore Initiative for Europe (LCIE) – Monitoring of large carnivores. LCIE.

LCIE 2018. Policy Support Statements of the Large Carnivore Initiative for Europe (LCIE) – Studying large carnivores with telemetry for their conservation in Europe. LCIE.

Leigh J. & Chamberlain M.J. 2007. Effects of aversive conditioning on behavior of nuisance Louisiana black bears. Louisiana State University 2: 1–45. https://doi.org/10.2307/24875663.

Linnell J., Salvatori V. & Boitani L. 2008. Guidelines for population level management plans for large carnivores in Europe. A Large Carnivore Initiative for Europe report prepared for the European Commission, contract 070501/2005/424162/MAR/B2. European Commission, contract N°070501/2005/424162/MAR/B2.

Linnell J.D.C. 2013. From conflict to coexistence? Insights from multi- disciplinary research into the relationships between people, large carnivores and institutions. European Commission Series, European Commission Series. European Commission, contract N°070307/2012/629085/SER/B3.

Linnell J.D.C., Swenson J.E., Landa A. & Kvam, T. 1998. Methods for monitoring European large carnivores - A worldwide review of relevant experience. NINA Oppdragsmelding 549.

MAFF (Ministry of Agriculture, Food and Forestry) 2001. Regulation of Hunting and Game Conservation Act. Chapter four: Game management and conservation; Section I: Game management. Art 51. Accessed at https://www.lex.bg/laws/ldoc/-12290559.

Majić Skrbinšek A. & Krofel M. 2013. Defining, preventing and reacting to problem bear behaviour in Europe. Final report for the pilot action to DG Environment, European Commission, Bruxelles. Contract (07.0307), p. 654446.

Martin J., Basille M., Van Moorter B., Kindberg J., Allainé D. & Swenson J. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). Canadian Journal of Zoology 88: 875–883. https://doi.org/10.1139/z10-053.

Moa P., Negård A., Overskaug K. & Kvam T. 2001. Possible Effects of the Capture Event on Subsequent Space Use of Eurasian Lynx. Wildlife Society Bulletin 29: 86–90.

Mohorović M., Krofel M. & Jerina K. 2017. Review of Brown bear (*Ursus arctos*) habitat selection in relation to anthropogenic disturbances. Acta silvae ligni 113: 14–28. https://doi.org/10.20315/asetl.113.2.

Morellet N., Verheyden H., Angibault J.-M., Cargnelutti B., Lourtet B. & Hewison M.A.J., 2009. The Effect of Capture on Ranging Behaviour and Activity of the European Roe Deer *Capreolus capreolus*. Wildlife Biology 15: 278–287. https://doi.org/10.2981/08-084.

Nellemann C., Støen O.-G.G., Kindberg J., Swenson J.E., Vistnes I., Ericsson G., Katajisto J., Kaltenborn B.P., Martin J. & Ordiz A. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. Biological Conservation 138: 157–165. https://doi.org/10.1016/j.biocon.2007.04.011

Northrup J.M., Anderson C.R. & Wittemyer G. 2014. Effects of helicopter capture and handling on movement behavior of mule deer. Journal of Wildlife Management 78: 731–738. https://doi.org/10.1002/jwmg.705.

Ordiz A., Moen G.K., Sæbø S., Stenset N., Swenson J.E. & Støen O.-G. 2019. Habituation, sensitization, or consistent behavioural responses? Brown bear responses after repeated approaches by humans on foot. Biological Conservation 232: 228–237. https://doi.org/10.1016/j.biocon.2019.01.016.

Rode K.D., Farley S.D. & Robbins C.T. 2006. Behavioural responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation 133: 70–80. https://doi.org/10.1016/j.biocon.2006.05.021.

Rode K.D., Pagano A.M., Bromaghin J.F., Atwood T.C., Durner G.M., Simac K.S. & Amstrup S.C. 2014. Effects of capturing and collaring on polar bears: findings from long-term research on the southern Beaufort Sea population. Wildlife Research 41: 311. https://doi.org/10.1071/wr13225.

Selva N., Teitelbaum C.S., Sergiel A., Zwijacz-Kozica T., Zieba F., Bojarska K. & Mueller T. 2017. Supplementary ungulate feeding affects movement behaviour of brown bears. Basic and Applied Ecology 24: 68–76. https://doi.org/10.1016/j.baae.2017.09.007.

Skinner B.F. 1963. Operant behaviour. American Psychologist 18: 503–515. https://doi.org/10.1037/h0045185.

Smith R. 2001. Animal research: the need for a middle ground. British Medical Journal 322: 248–249.

Spraker T.R. 1993. Stress and capture myopathy in artiodactyls. In: Fowler M.E. (Ed.). Zoo and Wild Animal Medicine: Current Therapy. 3rd ed. Philadelphia: W.B. Saunders Co, pp. 481–488.

Travaini A., Aldama J. & Delibes M. 1993. Red fox capture locations in relation to home range boundaries. Mammalia 57: 448–451.

Wall J. 2014. Movement Ecology Tools for ArcGIS (ArcMET) 10.3.1 v1.

Wesson J.A., Scanlon P.F., Kirkpatrick R.L., Mosby H.S & Butcher R.L. 1979. Influence of chemical immobilization and physical restraint on steroid hormone levels in blood of white-tailed deer. Canadian Journal of Zoology 57: 768–776. PMID: 519551.

Received: 06.08.2020
Accepted: 01.12.2020