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**Anthropogenic food resources foster the coexistence of distinct life history
strategies: year-round sedentary and migratory brown bears**

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Abstract: Plastic behavioral adaptation to human activities can result in the enhancement and establishment of distinct behavioral types within a population. Such inter-individual behavioral variations, if unaccounted for, can lead to biases in our understanding of species' feeding habits, movement pattern, and habitat selection. We tracked the movements of 16 adult brown bears in a small and isolated population in northeast Turkey to i) identify inter-individual behavioral variations associated with the use of a garbage dump and ii) to examine how these variations influenced ranging patterns, movements behavior and habitat selection. We identified two remarkably distinct behavioral types: bears that regularly visited the dump and remained sedentary year-round, and bears that never visited the dump and migrated 165.7 ± 20.1 km (round-trip mean cumulative distance \pm SE) prior to hibernation to search for food. We demonstrated that during migratory trips, bears moved more rapidly and were less selective in habitat choice than during the sedentary phase; during the migration phase forest cover was the only important environmental characteristic. Our results thus reinforce the growing evidence that animals' use of the landscape largely changes according to movement phase. Our study shows that anthropogenic food resources can influence food habits, which can have cascading effects on movement patterns and hence habitat selection, ultimately resulting in the establishment of distinct behavioral types within a population. Identification and consideration of these behavioral types is thus fundamental for the correct implementation of evidence-based conservation strategies at the population level.

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1 **Anthropogenic food resources foster the coexistence of distinct life history strategies:**
2 **year-round sedentary and migratory brown bears**

3

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11 **Running title:** Bear migration and movements in a human-dominated landscape

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14

15 **ABSTRACT:**

16 Plastic behavioral adaptation to human activities can result in the enhancement and
17 establishment of distinct behavioral types within a population. Such inter-individual
18 behavioral variations, if unaccounted for, can lead to biases in our understanding of species'
19 feeding habits, movement pattern, and habitat selection. We tracked the movements of 16
20 adult brown bears in a small and isolated population in northeast Turkey to i) identify inter-
21 individual behavioral variations associated with the use of a garbage dump and ii) to examine
22 how these variations influenced ranging patterns, movements behavior and habitat selection.
23 We identified two remarkably distinct behavioral types: bears that regularly visited the dump
24 and remained sedentary year-round, and bears that never visited the dump and migrated 165.7
25 ± 20.1 km (round-trip mean cumulative distance \pm SE) prior to hibernation to search for food.
26 We demonstrated that during migratory trips, bears moved more rapidly and were less
27 selective in habitat choice than during the sedentary phase; during the migration phase forest
28 cover was the only important environmental characteristic. Our results thus reinforce the
29 growing evidence that animals' use of the landscape largely changes according to movement
30 phase. Our study shows that anthropogenic food resources can influence food habits, which
31 can have cascading effects on movement patterns and hence habitat selection, ultimately
32 resulting in the establishment of distinct behavioral types within a population. Identification
33 and consideration of these behavioral types is thus fundamental for the correct
34 implementation of evidence-based conservation strategies at the population level.

35

36 **KEY WORDS:** anthropogenic food resource; behavioral type; habitat selection; migration;
37 movement modes; *Ursus arctos*.

38

39

40 **INTRODUCTION**

41 As a result of increasing human pressure, many wildlife species live in modified and
42 fragmented landscapes (Hanski, 1999; Goudie, 2013). To cope with novel and constantly
43 changing environments, cognitively complex species may develop plastic strategies (Valeix *et*
44 *al.*, 2012; Sol, Lapiendra & González-Lagos, 2013, Flack *et al.*, 2016), which can result in the
45 establishment of distinct alternative behaviors (hereafter behavioral types) within a population
46 (Gill, Norris & Sutherland, 2001; Elfström *et al.*, 2014). Such inter-individual variation in
47 behavioral types, if unaccounted for, can lead to biases in our understanding of species' life
48 history traits, movement pattern and habitat selection (Elliot *et al.*, 2014; Weimerskirch *et al.*,
49 2015). Therefore, careful identification and consideration of observed variation in behavioral
50 types is fundamental for the correct implementation of evidence-based conservation strategies
51 at the population level.

52 Animal behavior, life history, movement patterns and habitat selection can be
53 influenced by environmental variations (Nelson, 1998; Stien *et al.*, 2010), by changes during
54 different stages of the life cycle, such as the transition from a sedentary to a dispersing
55 movement mode (Elliot *et al.*, 2014), and by anthropogenic activities (Ordiz *et al.*, 2013,
56 Flack *et al.*, 2016). For example, the access to additional food sources resulted in a
57 subpopulation of otherwise migrant white storks (*Ciconia ciconia*) to remain resident year-
58 round (Massemim-Challet *et al.*, 2006). Similarly, spatiotemporal variation in anthropogenic
59 food resources influenced black-tailed gull (*Larus crassirostris*) foraging trips and selection
60 of feeding grounds during the incubation and hatching period (Yoda *et al.*, 2012). Changes in
61 feeding habits, movement patterns and habitat selection thus provide us with a dynamic
62 insight in the animal's sensitivity and adaptation to anthropogenic activities and alteration of
63 the landscape. Information on movement patterns and habitat selection during long-distance
64 movements can help us further understand a species' requirements during different stages and

under changing environmental conditions. This knowledge is necessary to model movement of individuals among habitat fragments, implement evidence-based plans to create wildlife corridors, and promote connectivity among populations (Palmer, Coulon & Travis, 2014; Runge *et al.*, 2014).

A species that shows remarkable adaptation to human-altered landscapes is the brown bear (*Ursus arctos*). Bears are well known to complement their diet at garbage dumps, campsites and residential areas. The frequent use of these human-related food resources often leads to individual bears becoming ‘problem’ animals, which are frequently relocated or killed by management agencies (Peirce & Van Daele 2006). The access to artificial food resources has been reported to reduce bears home range size (Blanchard & Knight, 1991), despite home range in wild bears is typically not directly influenced by food availability (Dahle & Swenson, 2003). Human activity and disturbance further influence the spatiotemporal use of resources and movement patterns (Martin *et al.*, 2010; Ordiz *et al.*, 2013). The bears’ behavioral plasticity and individual opportunistic behavior may thus result in the establishment of alternative life history traits, such as alternative feeding strategies, movement patterns and habitat selection among individuals with access to artificial food resources.

The aim of this study was to investigate the effects of an anthropogenic food resource, a city garbage dump, on feeding and ranging patterns of a small and isolated subpopulation of bears in northeastern Turkey. In particular, we examined whether all bears used the dump to the same extent or whether they exhibited distinct feeding strategies. We expected that, if distinct feeding strategies were established within the population, they should be reflected in distinct spatial and movement patterns. We therefore tested for differences in movement patterns and movement parameters, and investigated habitat selection between quantitatively distinct sections of the entire path (i.e., the chronological collection of all its GPS locations)

90 of each individual. The obtained information was crucial for the implementation of local
91 management interventions, as there were governmental plans for closing the dump, with
92 predicted imminent changes in the bears' foraging strategies. Our results on habitat selection
93 have also imminent conservation implications, as they will be used to optimize the design of
94 the first wildlife corridor in Turkey, whose globally important biodiversity and wildlife
95 populations are experiencing a major conservation crisis (Şekercioğlu *et al.*, 2011).

96

97 METHODS

98 **Study Area**

99 The core study area ($\sim 550 \text{ km}^2$) was located in northeast Turkey and included the Sarıkamış
100 Forest Allahuekber Mountains National Park (hereafter SAMNP) and the surrounding
101 landscape (Fig. 1). The climate is continental, with temperate summer months during June–
102 September (average monthly: 13–18°C), and cold winter months with snowfalls during
103 November–March (average monthly: -10–0°C).

104 SAMNP covers an area of 225.2 km^2 , but only 49.69 km^2 is forested (Capitani *et al.*,
105 2015). The remaining 278.7 km^2 of forest is not protected, for a total forest cover of 328.4
106 km^2 (hereafter Sarıkamış forest). Sarıkamış forest is almost exclusively composed of Scots
107 pine (*Pinus sylvestris*). Open pastures and arable land surround patches of forest (Fig. 1).
108 Sarıkamış forest is fragmented, and is heavily used for logging, grazing, harvesting and
109 recreation. The understory vegetation is over-exploited, with consequent food scarcity for
110 grazers (Capitani *et al.*, 2015) and frugivorous species. Wild ungulate prey species are very
111 rare (Capitani *et al.*, 2015). Wolves (*Canis lupus*) and Caucasian lynx (*Lynx lynx dinniki*) also
112 inhabit the study area (Capitani *et al.*, 2015; Chynoweth, Coban & Şekercioğlu, 2015).
113 Although a viable bear population is known to occur ca. 100 km away in the Black Sea

114 forests (Can & Togan, 2004), no information was available on the bear population in the
115 SAMNP region prior to this study.

116 Additional fragmented patches of forest are scattered throughout the landscape
117 considerably far (> 12 km) from Sarıkamış forest (Fig. 1). Together with their surrounding
118 landscape, these forest remnants formed the extended study area of approximately 5000 km².
119 This extended area enclosed all locations visited by the bears during long distance movements
120 outside the core study area (see below).

121 In the middle of the core study area is the city of Sarıkamış (E 42.595°, N 40.332°)
122 with a population of 18,000 inhabitants (Fig. 1). An unfenced garbage dump lies about 3 km
123 west of the outskirts of Sarıkamış and represents a year-round additional source of food (Fig.
124 1). Bears are known to visit the dump at night and feed on food scraps (pers. obs.). The
125 proportion of the bear population visiting the dump and its effects on foraging behavior,
126 movements, and demographic traits were not previously investigated.

127

128 ***Fieldwork and collection of GPS movement data***

129 We captured and collared ten adult males and six adult females from a small and isolated
130 population in northeastern Turkey between September 2012 and June 2014. Immobilized
131 bears were fitted with GPS/GSM or GPS/Iridium radio-collars (*GPS Plus*, Vectronic
132 Aerospace GmbH, Germany) programmed to record one GPS location every hour. Bears were
133 monitored for a mean duration of 296 days (range: 125 –590 days). GPS acquisition rate was
134 > 90% for 15 out of 16 individuals; one collar consistently performed poorly (acquisition rate
135 ≈ 50%) (Online Supplementary Material, Appendix 1). To avoid including inaccurate GPS
136 locations in the dataset, we removed all locations with a position dilution of precision (PDOP)
137 > 10 (Elliot *et al.*, 2014). During the winter, when bears hibernate in caves or holes
138 (interquartile range: from November 23rd – December 3rd to March 6th – April 1st), the GPS

139 typically failed to acquire satellites; therefore, in the analyses, we only used each individual's
140 location data collected pre and post individual hibernation date.

141

142 ***Identification of inter-individual variation in the use of the garbage dump***

143 For each bear and for each year, we summed the number of GPS locations at the garbage
144 dump each month. We used a generalized additive mixed model (GAMM) framework to
145 investigate the relationship between month and the number of locations at the dump, while
146 allowing for potential nonlinear relationships (Wood, 2006). We entered individual gender
147 (Appendix 1) as categorical covariate, whereas we treated individual identity as random
148 intercept. This approach allowed us to identify two distinct categories. In subsequent
149 analyses, we therefore investigated and compared movement modes, movement pattern, and
150 habitats selection between these two categories.

151

152 ***Investigation of movement modes and sub-division in discrete movement phases***

153 To investigate whether the two different categories exhibited different movement modes, we
154 fitted four competing a-priori-defined functions representing alternative movement modes to
155 the entire path of each collared bear. The four movement modes were as follow: (i) year-
156 round residency, (ii) dispersal, (iii) migration, and (iv) nomadism (*sensu* Börger & Fryxell,
157 2012) (Fig. 2). This analytical method relies on the net squared displacement statistics
158 combined with a non-linear hierarchical modeling framework (Börger & Fryxell, 2012).
159 Appendix 2 provides a detailed mathematical and visual representation. We developed an
160 additional metric to ensure that the NSD did not assign long-distance movement modes such
161 as migration to small-scale movement patterns occurring at the local scale. For each
162 individual, we calculated the ratio between the maximum and the median of the observed net
163 displacement (ρ). In this metric the maximum net displacement for migrating individuals

164 should increase faster than the median, thus increasing the value of ρ . Empirical evidence
165 suggested that $\rho > 5$ corresponded to actual migration events; while ρ between 1.5 and 2.5
166 were typical of individuals moving at the local scale (Fig. 2, Appendix 1).

167 In a second step, we visually sub-divided the movement mode of each individual in
168 discrete movement phases: (i) sedentary, (ii) roaming, and (iii) stopover (Fig. 2). For
169 example, an individual characterized by year-round residency was assigned a sedentary phase
170 for its entire path (Fig. 2). On the other hand, the entire path of a migrating individual was
171 chronologically divided into sedentary, roaming, stopover (the final site of the migratory trip),
172 roaming, and sedentary phases (Fig. 2). Here, migration refers to a particular movement mode
173 and hence to an entire movement trajectory, and not to the actual displacement phase between
174 two distinct geographic areas, which we define as the roaming phase. We then investigated
175 differences in movement parameters and habitat selection between the three different
176 movement phases between and within the two distinct bear categories (see *Calculation of*
177 *movement parameters and Step selection function*).

178

179 ***Calculation of movement parameters***

180 We first investigated differences in movement parameters (i.e., step length and turning
181 angles) between day and night, as bears in European human-dominated landscapes are known
182 to be predominantly nocturnal (Kaczensky *et al.*, 2006). Only consecutive locations 1 hour
183 apart were considered. Due to the considerable differences detected between the dial periods,
184 we recalculated movement parameters for the sedentary, stopover, and roaming phases using
185 night-only data.

186 In a subsequent step, we investigated differences in step length between the two bear
187 categories and across the three movement phases using a mixed-effects model. We included
188 sex and season as additional categorical covariates, and individual as random intercept. The

189 inclusion of season as covariate to control for seasonal effects was due to the fact that the
190 roaming and stopover phases were highly seasonal, and thus differences in step lengths
191 between these two phases and the sedentary phase could have arisen through seasonal
192 differences instead of through genuine differences among movement phases.

193

194 ***Step selection function***

195 We used a step selection function (SSF) framework (Fortin *et al.*, 2005) to infer the effects of
196 landscape structures on bear movements during the sedentary, stopover and roaming phases.
197 For each phase, we pooled the data irrespective of bear category. Step selection functions
198 typically assume an exponential function of the form:

$$w(\mathbf{X}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n)$$

199 where β_i are the coefficients estimated by conditional logistic regression associated with
200 landscape variables x_i . Steps with higher SSF scores $w(\mathbf{X})$ are more likely to be chosen by the
201 animals (Fortin *et al.*, 2005), and $\beta = 0$ indicates absence of selection (Forester *et al.*, 2009).
202 For each observed step, we created a set of 10 alternative steps; the end of these steps
203 represented alternative locations that the animal could have chosen. A step is here defined as
204 the vector between two consecutive locations. Step length refers to the Euclidean distance
205 between consecutive locations. Following Fortin et al. (2005), these alternative steps were
206 created by drawing step length and turning angles from movement-phase-specific empirical
207 distributions built with data collected from the other monitored individuals (see Appendix 3
208 for more details).

209 Landscape characteristics at the observed locations were regressed against those at the
210 alternative locations. Landscape characteristics included distance to the nearest village,
211 distance to the nearest paved road, altitude, slope, aspect, and forest cover (Appendix 3).
212 Because selection partially depends on the scale at which a resource is distributed in the

213 landscape, a linear variable “distance to the previous location” was included in the model to
214 increase the robustness of our analysis (Forester, Im & Rathouz, 2009). We implemented a
215 two-stage approach using the *TwoStepClogit* package (Craiu *et al.*, 2011) in R (The R
216 Foundation for Statistical Computing; version 3.0.3) to allow for differential habitat selection
217 responses among individuals (Fieberg *et al.*, 2010). We removed GPS locations at the garbage
218 dump from the analysis of the effect of landscape structure on the bears’ habitat selection.
219 This was because the dump is not a feature characteristic of the entire landscape, and
220 including these locations would have resulted in an over-representation (i.e., inflated
221 selection) of the environmental variables (such as forest cover) at the dump. We followed the
222 10-fold cross-validation procedure suggested by Boyce *et al.* (2002) to examine model
223 performance (see Appendix 3 for more details).

224

225 **RESULTS**

226 ***Inter-individual variation in the use of the garbage dump***

227 We observed two categories of individuals: bears that visited the dump (hereafter dump bears)
228 and bears that never did (hereafter wild bears). Dump bears included three females and seven
229 males; wild bears included three females and three males. Visits at the dump significantly
230 varied across months ($F_{\text{edf}=5.1} = 8.93$, $p < 0.001$) but not between gender ($t = 1.5$, $p = 0.13$).
231 Visits increased towards the second half of the year (> 40% increase between March and
232 September) and peaked in late August (Fig. 3). Dump bears hibernated on average three days
233 after wild bears (November 25th and November 22nd respectively), suggesting that this life
234 history trait is not influenced by the use of the dump. We captured three dump bears in the
235 forest 5.7, 7.2 and 10.1 km from the dump, and we observed three wild bears in the vicinity
236 of, but never at, the dump (closest recorded location 0.5, 1.3, 2.0 km). We therefore

237 concluded that capture site locations did not explain the existence of the two observed
238 categories.

239

240 ***Movement modes***

241 All wild bears migrated outside Sarıkamış forest. Five individuals made long-distance
242 migratory trips characterized by a maximum linear displacement from the site of capture of 36
243 – 108 km, and lasted between 23 and 72 days. One male made a shorter migratory trip with a
244 maximum linear displacement of 17 km, which lasted only 7 days (Appendix 5). Overall, the
245 mean cumulative migratory round-trip distance was 165.7 ± 20.1 km. Migratory trips
246 occurred closely prior to hibernation between the mean dates September 18th (range: August
247 29th – September 30th) and November 1st (range: October 10th – December 11th) (Fig. 3). The
248 only exception was the male that did a shorter trip of 7 days in June. His collar stopped
249 recording GPS locations on October 9th, we cannot know whether this bear may have also
250 migrated after that date. We conservatively classified one wild male as nomadic (Appendix
251 4). His collar stopped working on November 11th and we therefore don't know whether or not
252 he had returned to Sarıkamış forest before hibernation.

253 Dump bears never migrated, with the exception of an old female that made a shorter
254 migratory trip of 27 km that lasted 13 days (Appendix 5). Given the short duration of this trip,
255 we cannot exclude that this was a prospecting trip rather than real migration. The same
256 applies to the wild male that made a short trip of seven days.

257

258 ***Movement parameters***

259 The distribution of step lengths and turning angles varied considerably between daytime and
260 nighttime (Fig. 4a,b). In particular, during the day, bears were characterized by turning angles
261 close to 180° and short steps (mean ± SE = 263 ± 5 m), which are typical of stationary (i.e.,

262 resting) or small-scale searching (e.g. feeding) behavior. To the contrary, at night, their
263 movement pattern was more directional with turning angles close to 0° and displacements
264 occurred at a quicker pace (mean ± SE = 535 ± 5 m). At night, the distribution of step lengths
265 and turning angles showed more consistent patterns across the three movement phases (Fig.
266 4c,d). Nevertheless, steps during the roaming phase appeared longer and more directional.

267 We did not detect differences in overall nighttime step lengths between wild and dump
268 bears ($F_{1,12} = 0.4$, $p = 0.52$) nor between gender ($F_{1,12} = 1.48$, $p = 0.25$). Step length differed
269 significantly among movement phases ($F_{2,34275} = 511.8$, $p < 0.001$). Irrespective of behavior
270 and sex, steps during the roaming phase were twice as long (predicted mean step length 940
271 m) than steps during the sedentary (439 m) and stopover (420 m) phase (Fig. 4e). We detected
272 a significant seasonal effect ($F_{2,34275} = 62.7$, $p < 0.001$) with a tendency towards shorter steps
273 late in the season, suggesting that the difference between the sedentary and roaming phases
274 did not depend on seasonal factors, but rather on genuinely different patterns during the
275 movement phases. If this was not the case, a reduction, rather than an increase, in step length
276 during the roaming phase should have been observed.

277

278 ***Habitat selection***

279 Results are based on data from wild and dump bears for the sedentary phase and on data from
280 wild bears for the roaming and stopover phase. At the population level, bears appeared to be
281 less ‘selective’ in their habitat choice during the roaming phase than they were during the
282 sedentary and stopover phase. During roaming, out of the six landscape variables, only the β
283 coefficient for forest had a value greater than 2 SE from 0 (Tab. 1). This indicates a
284 significant association between forest and the bears’ chosen paths. Nevertheless, we observed
285 high inter-individual variation for forest selection (Table 1).

286 During the sedentary phase, forest, slope and distance to roads significantly influenced
287 the animals' step selection (Tab. 1). The positive effect of slope and forest suggests that, at
288 the population level, animals sought forested locations and steeper slopes. The negative
289 relationship with distance to roads indicates that locations far away from roads were less
290 likely to be chosen. During the stopover phase bears preferred forest and locations far from
291 villages (Tab. 1). Based on 10-fold cross-validation procedure, our models provided excellent
292 fit for the sedentary phase ($r_s = 0.95$) and only moderate for the stopover ($r_s = 0.23$) and
293 roaming ($r_s = 0.12$) phase.

294

295 **DISCUSSION**

296 We defined two categories of bears based on high-resolution GPS data from 16 adult
297 individuals: dump bears (i.e. bears that regularly visited a garbage dump) and wild bears (i.e.
298 bears that never did). Substantial differences in movement patterns between dump and wild
299 bears allowed us to identify two distinct behavioral types. While dump bears were
300 characterized by year-round residency, wild bears undertook migratory round-trips > 100 km.
301 Our results thus showed that differences in life history traits within the study population were
302 associated with the exploitation of a human-related food source. To the best of our
303 knowledge, such behavioral dichotomy within a population of brown bears has never been
304 reported; and only a few cases are known for black bears (*Ursus americanus*) (Noyce &
305 Garshelis, 2011; Liley & Walker, 2015). Extreme variation in migratory behavior have been
306 shown to have direct energetic and fitness consequences (Weimerskirch *et al.*, 2015, Flack *et*
307 *al.*, 2016). Investigation of differences in key demographic parameters such as survival and
308 reproductive rate between the two behavioral types is therefore required to better understand
309 the population dynamics of the study system.

310 Migration is conceivably linked to a seasonal availability of resources, such as food
311 and mates (Dingle, 2014). Because migratory trips occurred right before hibernation and
312 because direct field investigation of the vegetation at migration stopover sites revealed a high
313 prevalence of oak forest (*Quercus spp.*) (as opposed to Sarıkamış forest which was entirely
314 composed of Scots pines; cfr. Appendix 5), we deduced that hyperphagia before the winter
315 drove the observed patterns (Noyce & Garshelis, 2011, Seger *et al.*, 2013). This hypothesis
316 was further corroborated by the fact that only wild bears (i.e. those bears that did not use the
317 additional food resources provided by the city garbage dump) migrated. Since migratory trips
318 occurred between September and November, we excluded mating activities (May – July) as
319 an alternative driver for the observed movement patterns. We found no comparable study
320 describing similar food-related migratory movements immediately before hibernation in
321 brown bears. Additionally, while long-distance movements of bears are typically associated
322 with dispersal or translocation events (Liley & Walker, 2015) the observed distances covered
323 by migrating wild bears were remarkable. Our findings thus add valuable information to the
324 life history of the species and a new spatiotemporal dimension to its management and to
325 conservation efforts.

326 The identification of two behavioral types and information on ranging patterns have
327 far-reaching implications for the regional management and conservation of the species. First,
328 the observed long-distance movements showed that bears living in the SAMNP are
329 potentially connected with the larger bear population of the Black Sea mountains and Georgia
330 (Can & Togan, 2004). Our data also provided further support for the ongoing efforts to create
331 Turkey's first wildlife forested corridor, with the goal of enhancing connectivity between the
332 SAMNP and wildlife populations in the Black Sea and Georgian forests. Second, the natural
333 resources of Sarıkamış forest may not be sufficient to sustain the local bear population
334 throughout the entire year. Bears had to migrate to find food outside the core study area or to

335 supplement their diet with anthropogenic food resources. Any intervention that would limit
336 either option could have severe consequences at the subpopulation level. Third, following a
337 governmental plan, the city garbage dump will be closed in the near future. We hypothesized
338 three scenarios: 1) dump bears die following malnutrition before hibernation, 2) they resume
339 the migratory behavior observed in forest bears, or 3) they seek food in the Sarıkamış city and
340 nearby villages. Given the bears' ability to exploit anthropogenic food resources (Elfström *et*
341 *al.*, 2012), we anticipate the third scenario, at least in the short term, which is likely to
342 increase the interactions and existing conflicts with people (Chynoweth *et al.*, 2016). To limit
343 interactions and avoid fatalities, the closure of the dump should therefore be coupled with the
344 measures such as the use of bear-proof bins and daily removal of household leftovers
345 (Robbins, Schwartz & Felicetti, 2004). In the long term, after the dump closure, the
346 persistence of the bear population of the Sarıkamış forest will depend on the bears' migratory
347 possibility. Conservation efforts should therefore aim to secure and facilitate their migratory
348 movements to the foraging grounds prior to hibernation. Given the population-level selection
349 for forested habitat, this can be achieved through the reforestation of the proposed wildlife
350 corridor and should be accompanied by education efforts to enhance bear acceptance by the
351 local population along the observed migratory route.

352 We also demonstrated that animals' movements and use of the surrounding landscape
353 largely depend on their movement phase. Our study thus provides further evidence that the
354 source of the data used to model animals' habitat selection is as important as the type of
355 predictor environmental variables considered (Zeller, McGarigal & Whiteley, 2012; Elliot *et*
356 *al.*, 2014). We showed that during the roaming phase bears were less selective in their habitat
357 choice compared to the sedentary phase. Differences in habitat selection between resident and
358 roaming individuals (in the specific case of dispersers) have been reported for other species
359 (Elliot *et al.*, 2014; Killeen *et al.*, 2014). While during the sedentary phase individuals may

360 select habitats based on the ‘known’ distribution of food, shelter, and mates, during the
361 roaming phase they are more naïve to the landscape matrix they move through. Forest
362 appeared, however, to be equally important in each phase. Being a prominent landscape
363 feature, forest can be easily recognized in the distance during migratory trips through
364 unknown landscapes, and actively selected for. The selection of locations closer to roads
365 during the sedentary phase around Sarıkamış forest may be due to the presence of additional
366 food resources deriving from intensive picnic activities (pers. obs.), but further investigation
367 is necessary. Including non-linear responses of distance to roads, but also of distance to
368 villages and elevation, could help further understand mechanisms of habitat selection. We
369 caution for over interpretation of the results for the roaming and stopover phase due to the
370 moderate model performance (see Appendix 3 for further considerations).

371 To summarize, we showed that the availability of a human-related source of food can
372 cause a behavioral dichotomy among individuals of a confined population. This inter-
373 individual variation is manifested in alternative feeding habits, movement pattern and
374 selection of different habitat types. Therefore, identification and consideration of observed
375 variation in behavioral types is fundamental for the correct implementation of evidence-based
376 conservation strategies. Failures to detect such differences could result in the erroneous
377 allocation of limited conservation resources, such as setting aside portions of land
378 characterized by landscape features that are critical to only particular behavioral types
379 (Simberloff *et al.*, 1992; Beier & Noss, 2008). Finally, because most research on brown bears
380 has been carried out in northern Europe and North America, this work in Turkey increases our
381 understanding of the species living under considerably different environmental, ecological,
382 and social conditions. Empirical evidence from this work thus adds valuable information for
383 the implementation of management and conservation strategies of bears in Turkey but also
384 worldwide.

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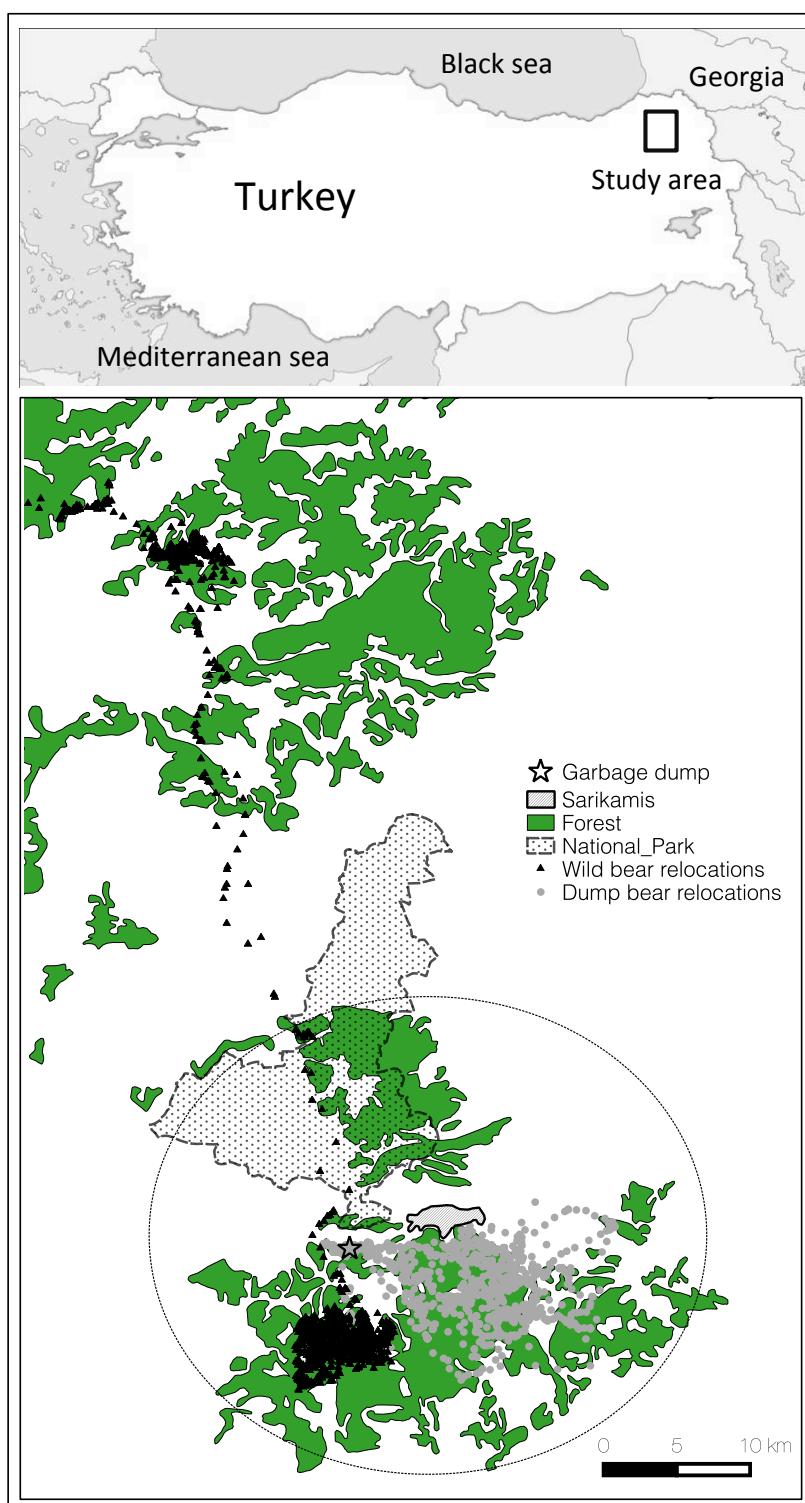
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524 **FIGURES AND TABLES**

525 Figure 1: The study area in northeastern Turkey. The dotted ellipse represents the core study
526 area including Sarikamış forest and surrounding pastures. The extended study area enclosed
527 all locations visited by the bears during migratory trips outside the core study area. GPS
528 relocations of one migrating bear (wild bear) and one bear resident all-year-round (dump
529 bear) are shown as an example.

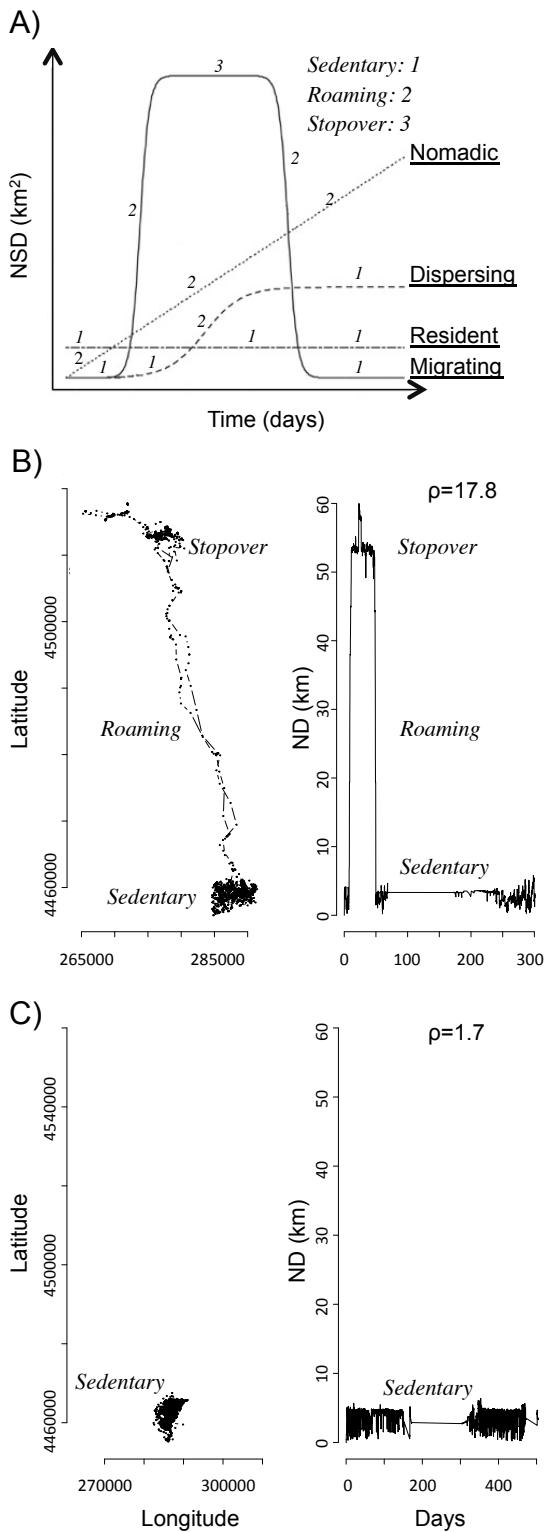


530 Figure 2: Characterization of movement trajectories by means of the net squared displacement
 531 approach. A) Graphical representation of four alternative movement modes (underlined) and

532 sub-division in three discrete movement phases

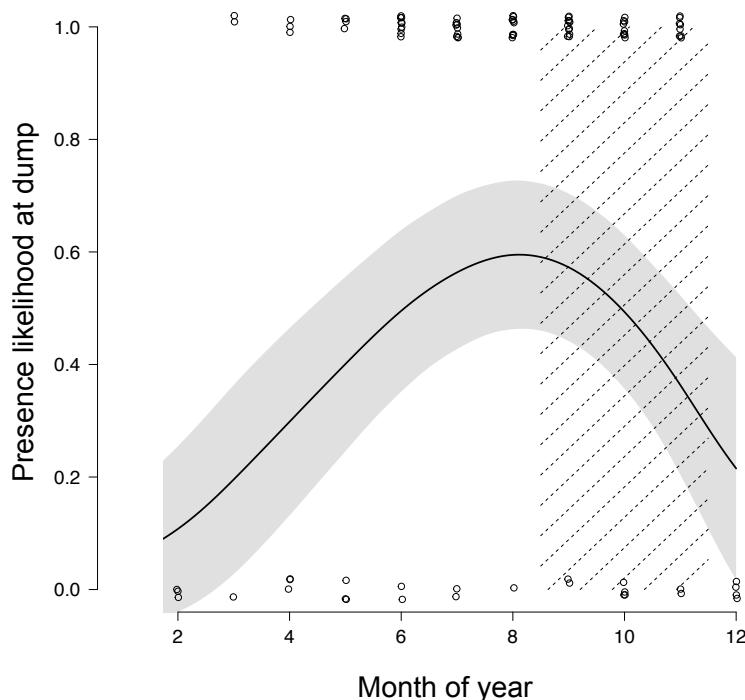
(italic) (modified from Bunnefeld et al. 2011).

For instance, a migratory movement mode is characterized by two sedentary phases, two roaming phases, and one (or more) stopover phase. A resident mode is characterized by a sedentary phase throughout the entire movement path. B) Observed trajectory corresponding to a migratory movement mode (left panel) and its corresponding ND (right). Discrete movement phases are shown. Each dot in the left panel represent a GPS location collected at hourly intervals; lines connect consecutive locations. In the right panel, horizontal net displacement sections represent the hibernation period C) Observed trajectory corresponding to a resident movement mode (left) and its corresponding ND (right). ρ are given for both movement modes: a low value indicates small-scale movements (see main text for further details).



555 Figure 3: Presence likelihood at the city garbage dump across a year. Confidence intervals are
556 shown in grey. Bears that visited the dump (dump bears) remained resident year-round. On
557 the other side, bears that never visited the dump (wild bears) migrated before hibernation; the
558 hatched area shows the migration period.

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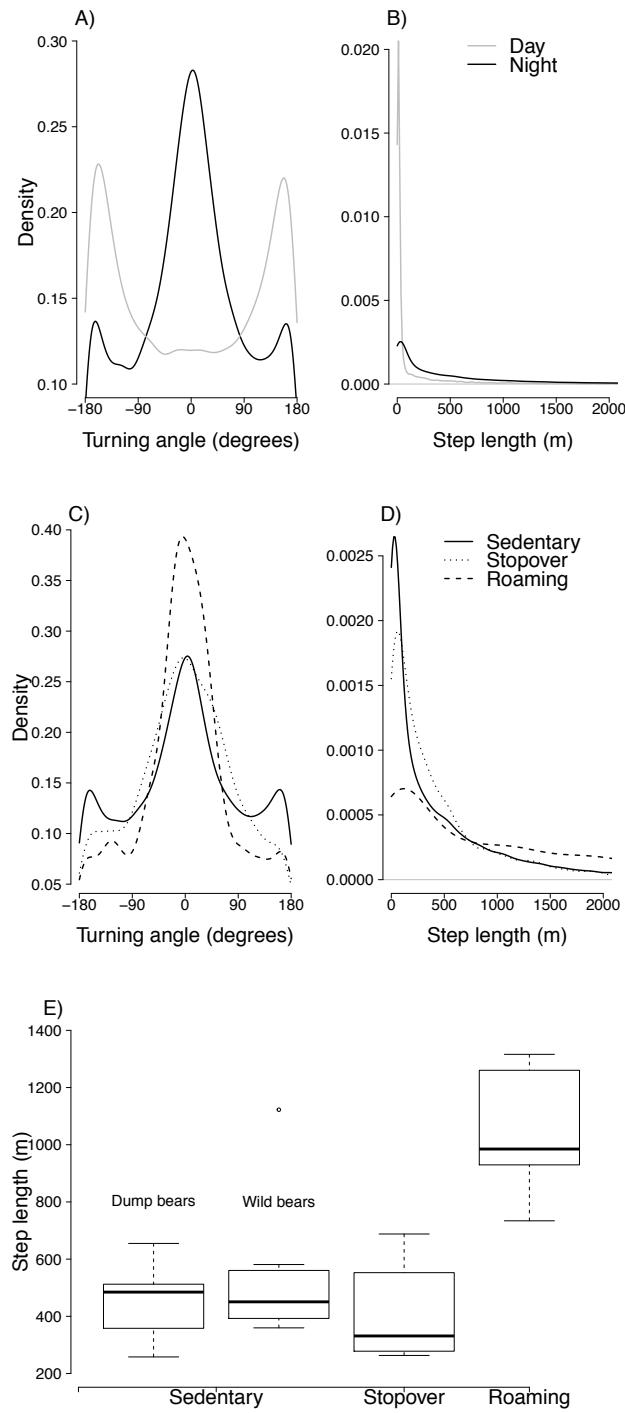
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569 Figure 4: Changes in movement parameters (i.e. step length and turning angle) between day
 570 and night (A, B), and among different movement phases at night (C-E). In panels C and D
 571 sedentary phase data of dump and wild bears are pooled. Panel E shows differences between
 572 dump and wild bears (the latter do not have a migratory and stopover phase).



573

574 Table 1: Population level coefficients, estimated standard errors and variance of random
 575 coefficients from a mixed conditional logistic regression of movement steps on six different
 576 environmental variables during the sedentary, stopover, and roaming phases. Asterisks
 577 indicate values significantly different from 0. For the sedentary phase data from dump and
 578 wild bears were pooled.

	Sedentary phase			Stopover phase			Roaming phase		
	beta	SE	Var	beta	SE	Var	beta	SE	Var
Distance to previous	-0.000326	0.00019	5.5e-07	-0.000376	0.00038	8.5e-07	0.000047	0.00012	8.4e-08
Altitude	0.000828	0.00069	5.1e-06	-0.000176	0.00087	2.8e-06	0.001629	0.00136	1.1e-05
Slope	0.012802*	0.00273	5.1e-05	-0.002962	0.0028	2.1e-06	0.008096	0.00877	2.9e-04
Aspect	-0.000156	0.00014	4.7e-08	0.000536	0.00035	1.9e-07	-0.000019	0.0004	1.5e-07
Forest	0.262084*	0.09703	1.0e-01	0.393145*	0.16658	8.7e-02	0.368015*	0.13588	1.9e-02
Distance to village	0.000154	0.00013	2.2e-07	0.000291*	0.00012	3.3e-08	-0.000055	0.00008	1.1e-08
Distance to road	-0.00024*	0.00009	8.8e-08	0.000001	0.00012	2.9e-08	0.000025	0.00006	1.4e-09

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