

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 north-east Turkey to (1) identify inter-individual behavioral variations associated with the use of a garbage dump and (2) 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 ± 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.

Introduction

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

the correct implementation of evidence-based conservation strategies at the population level.

Animal behavior, life history, movement patterns and habitat selection can be influenced by environmental variations (Nelson, 1998; Stien *et al.*, 2010), by changes during different stages of the life cycle, such as the transition from a sedentary to a dispersing movement mode (Elliot *et al.*, 2014), and by anthropogenic activities (Ordiz *et al.*, 2013; Flack *et al.*, 2016). For example, the access to additional food sources resulted in a subpopulation of otherwise migrant white storks *Ciconia ciconia* to remain resident year-round (Massemin-Challet *et al.*, 2006). Similarly, spatiotemporal variation in anthropogenic food resources influenced black-tailed gull *Larus crassirostris* foraging trips and selection of feeding grounds during the incubation and hatching period (Yoda *et al.*, 2012). Changes in feeding habits, movement patterns and habitat selection thus

provide us with a dynamic insight into an animal's sensitivity and adaptation to anthropogenic activities and alteration of the landscape. Information on movement patterns and habitat selection during long-distance 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 bear 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). Brown 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 north-eastern 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) of each individual. The obtained information was crucial for the implementation of local management interventions, as there were governmental plans for closing the dump, with predicted imminent changes in the bears' foraging strategies. Our results on habitat selection have also imminent conservation implications, as they will be used to optimize the design of the first wildlife corridor in Turkey (Şekercioğlu 2012), whose globally important biodiversity and wildlife populations are experiencing a major conservation crisis (Şekercioğlu *et al.*, 2011).

Materials and methods

Study area

The core study area (~550 km²) was located in north-east Turkey and included the Sarikamiş Forest Allahuekber Mountains National Park (hereafter SAMNP) and the surrounding

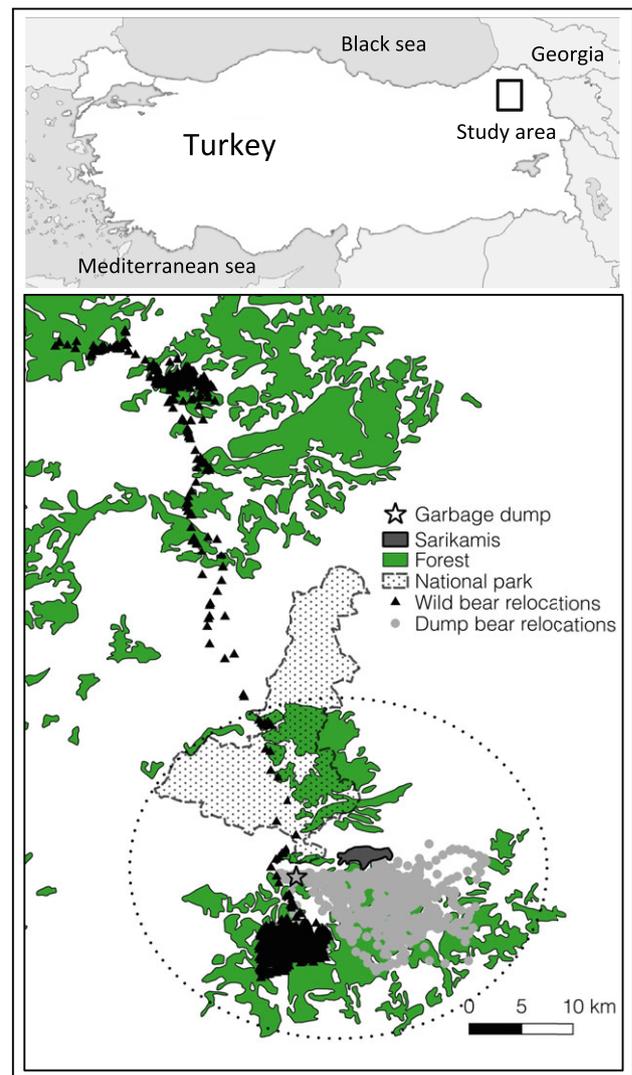


Figure 1 The study area in north-eastern Turkey. The dotted ellipse represents the core study area including Sarikamiş forest and surrounding pastures. The extended study area enclosed all locations visited by the bears during migratory trips outside the core study area. GPS relocations of one migrating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

landscape (Fig. 1). The climate is continental, with temperate summer months during June–September (average monthly: 13 to 18°C), and cold winter months with snowfalls during November–March (average monthly: –10 to 0°C).

SAMNP covers an area of 225.2 km², but only 49.69 km² is forested (Capitani *et al.*, 2016). The remaining 278.7 km² of forest is not protected, for a total forest cover of 328.4 km² (hereafter Sarikamiş forest). Sarikamiş forest is almost exclusively composed of Scots pine *Pinus sylvestris*. Open pastures and arable land surround patches of forest (Fig. 1). Sarikamiş forest is fragmented, and is heavily used for logging, grazing, harvesting and recreation. The understory vegetation is over-

exploited, with consequent food scarcity for grazers (Capitani *et al.*, 2016) and frugivorous species. Wild ungulate prey species are very rare (Capitani *et al.*, 2016). Wolves *Canis lupus* and Caucasian lynx *Lynx lynx dinniki* also inhabit the study area (Chynoweth, Coban & Şekerciöğlü, 2015; Capitani *et al.*, 2016). Although a viable bear population is known to occur ca. 100 km away in the Black Sea forests (Can & Togan, 2004), no information was available on the bear population in the SAMNP region prior to this study.

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

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

Fieldwork and collection of GPS movement data

We captured and collared 10 adult males and six adult females from a small and isolated population in north-eastern Turkey between September 2012 and June 2014. Immobilized bears were fitted with GPS/GSM or GPS/Iridium radio-collars (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) programmed to record one GPS location every hour. Bears were monitored for a mean duration of 296 days (range: 125–590 days). GPS acquisition rate was >90% for 15 out of 16 individuals; one collar consistently performed poorly (acquisition rate ≈ 50%) (Appendix S1). To avoid including inaccurate GPS locations in the dataset, we removed all locations with a position dilution of precision > 10 (Elliot *et al.*, 2014). During the winter, when bears hibernate in caves or holes (interquartile range: from November 23rd–December 3rd to March 6th–April 1st), the GPS typically failed to acquire satellites; therefore, in the analyses, we only used each individual's location data collected pre- and post-individual hibernation date.

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

For each bear and for each year, we summed the number of GPS locations at the garbage dump each month. We used a generalized additive mixed model framework to investigate the relationship between month and the number of locations at the dump, while allowing for potential nonlinear relationships (Wood, 2006). We entered individual gender (Appendix S1) as

categorical covariate, whereas we treated individual identity as random intercept. This approach allowed us to identify two distinct categories. In subsequent analyses, we therefore investigated and compared movement modes, movement pattern and habitat selection between these two categories.

Investigation of movement modes and subdivision in discrete movement phases

To investigate whether the two different categories exhibited different movement modes, we fitted four competing *a priori*-defined functions representing alternative movement modes to the entire path of each collared bear. The four movement modes were as follows: (1) year-round residency, (2) dispersal, (3) migration and (4) nomadism (*sensu* Börger & Fryxell, 2012; Fig. 2). This analytical method relies on the net squared displacement (NSD) statistics combined with a nonlinear hierarchical modeling framework (Börger & Fryxell, 2012). Appendix S2 provides a detailed mathematical and visual representation. We developed an additional metric to ensure that the NSD did not assign long-distance movement modes such as migration to small-scale movement patterns occurring at the local scale. For each individual, we calculated the ratio between the maximum and the median of the observed net displacement (ρ). In this metric, the maximum net displacement for migrating individuals should increase faster than the median, thus increasing the value of ρ . Empirical evidence suggested that $\rho > 5$ corresponded to actual migration events; while ρ between 1.5 and 2.5 were typical of individuals moving at the local scale (Fig. 2, Appendix S1).

In a second step, we visually sub-divided the movement mode of each individual in discrete movement phases: (1) sedentary, (2) roaming and (3) stopover (Fig. 2). For example, an individual characterized by year-round residency was assigned a sedentary phase for its entire path (Fig. 2). On the other hand, the entire path of a migrating individual was chronologically divided into sedentary, roaming, stopover (the final site of the migratory trip), roaming and sedentary phases (Fig. 2). Here, migration refers to a particular movement mode and hence to an entire movement trajectory, and not to the actual displacement phase between two distinct geographic areas, which we define as the roaming phase. We then investigated differences in movement parameters and habitat selection between the three different movement phases between and within the two distinct bear categories (see Calculation of movement parameters and Step selection function).

Calculation of movement parameters

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

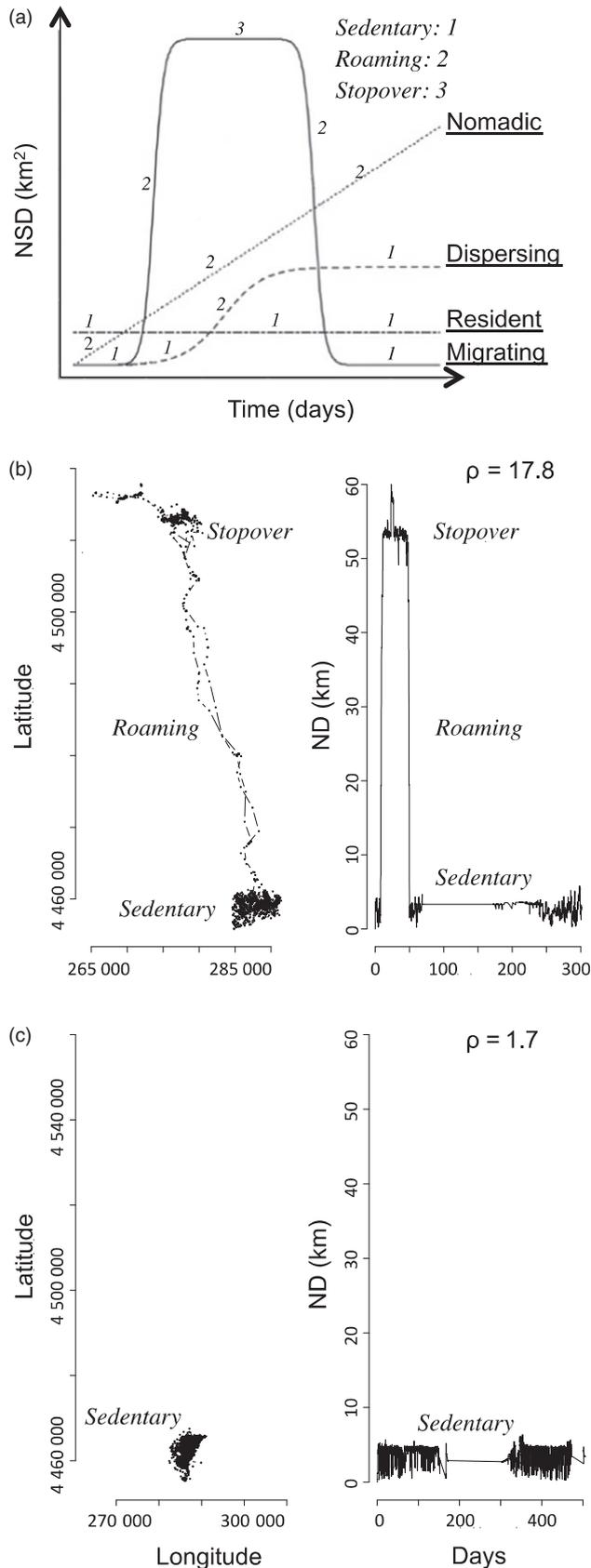


Figure 2 Characterization of movement trajectories by means of the net squared displacement approach. (a) Graphical representation of four alternative movement modes (underlined) and sub-division in three discrete movement phases (italic) (modified from Bunnefeld *et al.* 2011). For instance, a migratory 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).

In a subsequent step, we investigated differences in step length between the two bear categories and across the three movement phases using a mixed-effects model. We included sex and season as additional categorical covariates, and individual as a random intercept. The inclusion of season as covariate to control for seasonal effects was due to the fact that the roaming and stopover phases were highly seasonal, and thus differences in step lengths between these two phases and the sedentary phase could have arisen through seasonal differences instead of through genuine differences among movement phases.

Step selection function

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

$$w(X) = \exp(\beta_1 x_1 + \beta_2 x_2 \dots \beta_n x_n)$$

where β_i are the coefficients estimated by conditional logistic regression associated with landscape variables x_i . Steps with higher SSF scores $w(X)$ are more likely to be chosen by the animals (Fortin *et al.*, 2005), and $\beta = 0$ indicates absence of selection (Forester, Im & Rathouz, 2009). For each observed step, we created a set of 10 alternative steps; the end of these steps represented alternative locations that the animal could have chosen. A step is here defined as the vector between two consecutive locations. Step length refers to the Euclidean distance between consecutive locations. Following Fortin *et al.* (2005), these alternative steps were created by drawing step length and turning angles from movement phase-specific empirical distributions built with the data collected from the other monitored individuals (see Appendix S3, for more details).

Landscape characteristics at the observed locations were regressed against those at the alternative locations. Landscape characteristics included distance to the nearest village, distance

to the nearest paved road, altitude, slope, aspect and forest cover (Appendix S3). Because selection partially depends on the scale at which a resource is distributed in the landscape, a linear variable 'distance to the previous location' was included in the model to increase the robustness of our analysis (Forester *et al.*, 2009). We implemented a two-stage approach using the TwoStepClogit package (Craiu *et al.*, 2011) in R (The R Foundation for Statistical Computing; version 3.0.3) to allow for differential habitat selection responses among individuals (Fieberg *et al.*, 2010). We removed GPS locations at the garbage dump from the analysis of the effect of landscape structure on the bears' habitat selection. This was because the dump is not a feature characteristic of the entire landscape, and including these locations would have resulted in an over-representation (i.e. inflated selection) of the environmental variables (such as forest cover) at the dump. We followed the 10-fold cross-validation procedure suggested by Boyce *et al.* (2002) to examine model performance (see Appendix S3, for more details).

Results

Inter-individual variation in the use of the garbage dump

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

Movement modes

All wild bears migrated outside Sarikamiş forest. Five individuals made long-distance migratory trips characterized by a maximum linear displacement from the site of capture of 36–108 km, and lasted between 23 and 72 days. One male made a shorter migratory trip with a maximum linear displacement of 17 km, which lasted only 7 days (Appendix S5). Overall, the mean cumulative migratory round-trip distance was 165.7 ± 20.1 km. Migratory trips occurred closely prior to hibernation between the mean dates September 18th (range: August 29th–September 30th) and November 1st (range: October 10th–December 11th; Fig. 3). The only exception was the male that did a shorter trip of 7 days in June. His collar stopped recording GPS locations on October 9th, we cannot

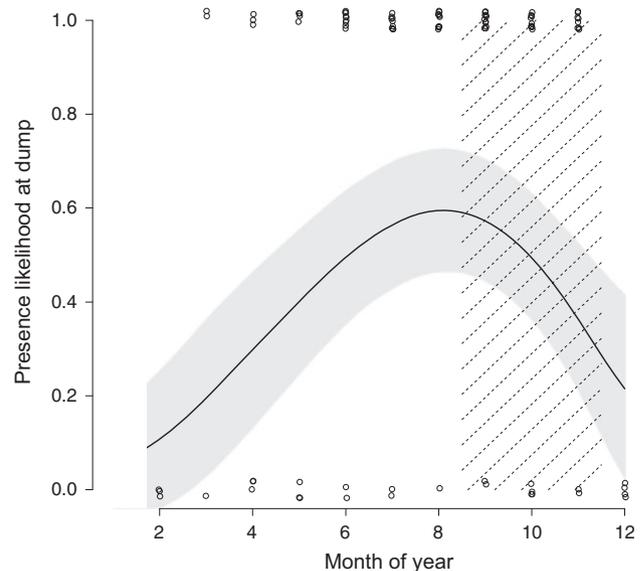


Figure 3 Presence likelihood at the city garbage dump across a year. Confidence intervals are shown in gray. Bears that visited the dump (dump bears) remained resident year-round. On the other side, bears that never visited the dump (wild bears) migrated before hibernation; the hatched area shows the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

know whether this bear may have also migrated after that date. We conservatively classified one wild male as nomadic (Appendix S4). His collar stopped working on November 11th and we therefore do not know whether or not he had returned to Sarikamiş forest before hibernation.

Dump bears never migrated, with the exception of an old female that made a shorter migratory trip of 27 km that lasted 13 days (Appendix S5). Given the short duration of this trip, we cannot exclude that this was a prospecting trip rather than real migration. The same applies to the wild male that made a short trip of 7 days.

Movement parameters

The distribution of step lengths and turning angles varied considerably between daytime and nighttime (Fig. 4a,b). In particular, during the day, bears were characterized by turning angles close to 180° and short steps (mean \pm SE = 263 ± 5 m), which are typical of stationary (i.e. resting) or small-scale searching (e.g. feeding) behavior. To the contrary, at night, their movement pattern was more directional with turning angles close to 0° and displacements occurred at a quicker pace (mean \pm SE = 535 ± 5 m). At night, the distribution of step lengths and turning angles showed more consistent patterns across the three movement phases (Fig. 4c,d). Nevertheless, steps during the roaming phase appeared longer and more directional.

We did not detect differences in overall nighttime step lengths between wild and dump bears ($F_{1,12} = 0.4$, $P = 0.52$) nor between gender ($F_{1,12} = 1.48$, $P = 0.25$). Step length differed significantly among movement phases ($F_{2,34} = 511.8$,

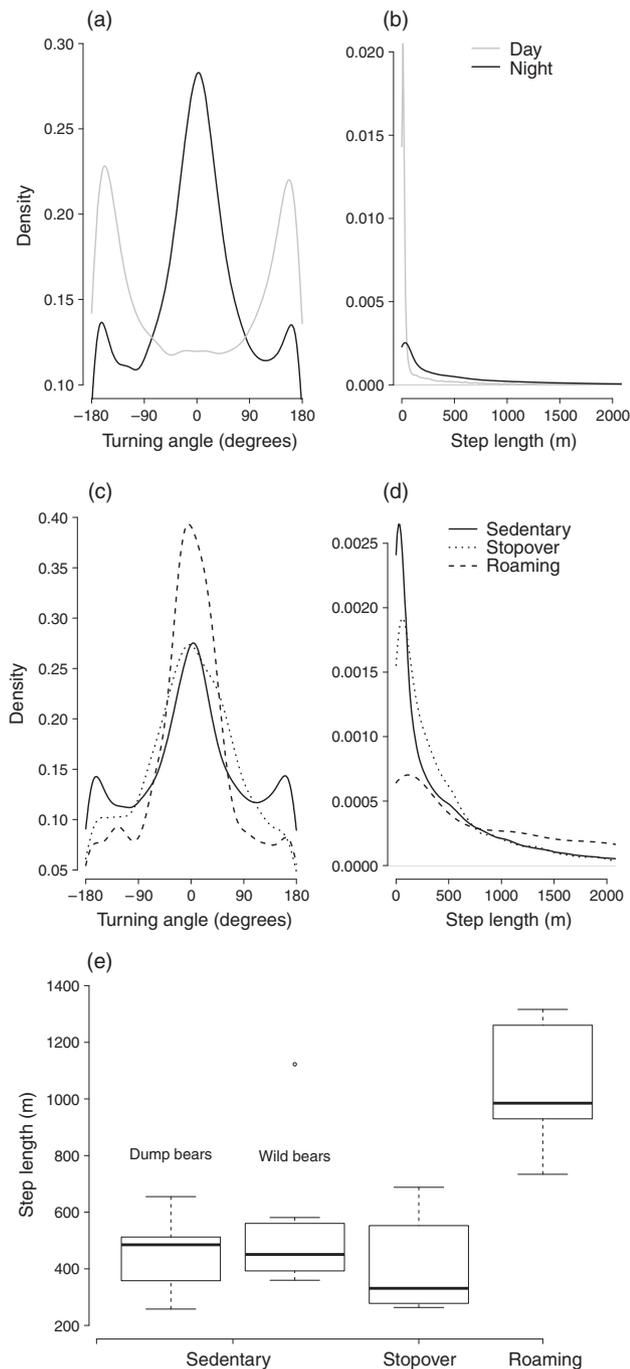


Figure 4 Changes in movement parameters (i.e. step length and turning angle) between day and night (a, b), and among different movement phases at night (c–e). In panels c and d, sedentary phase data of dump and wild bears are pooled. Panel e shows differences between dump and wild bears (the latter do not have a migratory and stopover phase).

$P < 0.001$). Irrespective of behavior and sex, steps during the roaming phase were twice as long (predicted mean step length 940 m) than steps during the sedentary (439 m) and stopover

(420 m) phase (Fig. 4e). We detected a significant seasonal effect ($F_{2,34} = 62.7$, $P < 0.001$) with a tendency toward shorter steps late in the season, suggesting that the difference between the sedentary and roaming phases did not depend on seasonal factors, but rather on genuinely different patterns during the movement phases. If this was not the case, a reduction, rather than an increase, in step length during the roaming phase should have been observed.

Habitat selection

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

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

Discussion

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

Migration is conceivably linked to a seasonal availability of resources, such as food and mates (Dingle, 2014). Because migratory trips occurred right before hibernation and because

Table 1 Population level coefficients, estimated standard errors and variance of random coefficients from a mixed conditional logistic regression of movement steps on six different environmental variables during the sedentary, stopover and roaming phases. For the sedentary phase, data from dump and wild bears were pooled

	Sedentary phase			Stopover phase			Roaming phase		
	β	SE	Var	β	SE	Var	β	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

*Values significantly different from 0.

direct field investigation of the vegetation at migration stopover sites revealed a high prevalence of oak forest *Quercus* spp., as opposed to Sarikamiş forest which is entirely composed of Scots pines (cf. Appendix S5), we deduced that hyperphagia before the winter drove the observed patterns (Noyce & Garshelis, 2011; Seger *et al.*, 2013). This hypothesis was further corroborated by the fact that only wild bears (i.e. those bears that did not use the additional food resources provided by the city garbage dump) migrated. Since migratory trips occurred between September and November, we excluded mating activities (May–July) as an alternative driver for the observed movement patterns. We found no comparable study describing similar food-related migratory movements immediately before hibernation in brown bears. Additionally, while long-distance movements of bears are typically associated with dispersal or translocation events (Liley & Walker, 2015), the observed distances covered by migrating wild bears were remarkable. Our findings thus add valuable information to the life history of the species and a new spatiotemporal dimension to its management and to conservation efforts.

The identification of two behavioral types and information on ranging patterns have far-reaching implications for the regional management and conservation of the species. First, the observed long-distance movements showed that bears living in the SAMNP are potentially connected with the larger bear population of the Black Sea mountains and Georgia (Can & Togan, 2004). Our data also provided further support for the ongoing efforts to create Turkey's first wildlife corridor (Şekerioğlu 2012), with the goal of enhancing connectivity between the SAMNP and wildlife populations in the Black Sea and Georgian forests. Second, the natural resources of Sarikamiş forest may not be sufficient to sustain the local bear population throughout the entire year. Bears had to migrate to find food outside the core study area or to supplement their diet with anthropogenic food resources. Any intervention that would limit either option could have severe consequences at the sub-population level. Third, following a governmental plan, the city garbage dump will be closed in the near future. We hypothesized three scenarios: (1) dump bears die following malnutrition before hibernation, (2) they resume the migratory behavior observed in forest bears or (3) they seek food in the Sarikamiş city and nearby villages. Given the bears' ability to exploit

anthropogenic food resources (Elfström *et al.*, 2012), we anticipate the third scenario, at least in the short term, which is likely to increase the interactions and existing conflicts with people (Chynoweth *et al.*, 2016). To limit interactions and avoid fatalities, the closure of the dump should therefore be coupled with the measures such as the use of bear-proof bins and daily removal of household leftovers (Robbins, Schwartz & Felicetti, 2004). In the long term, after the dump closure, the persistence of the bear population of the Sarikamiş forest will depend on the bears' migratory possibility. Conservation efforts should therefore aim to secure and facilitate their migratory movements to the foraging grounds prior to hibernation. Given the population-level selection for forested habitat, this can be achieved through the reforestation of the proposed wild-life corridor and should be accompanied by education efforts to enhance bear acceptance by the local population along the observed migratory route.

We also demonstrated that animals' movements and use of the surrounding landscape largely depend on their movement phase. Our study thus provides further evidence that the source of the data used to model animals' habitat selection is as important as the type of predictor environmental variables considered (Zeller, McGarigal & Whiteley, 2012; Elliot *et al.*, 2014). We showed that during the roaming phase bears were less selective in their habitat choice compared to the sedentary phase. Differences in habitat selection between resident and roaming individuals (in the specific case of dispersers) have been reported for other species (Elliot *et al.*, 2014; Killeen *et al.*, 2014). While during the sedentary phase individuals may select habitats based on the 'known' distribution of food, shelter and mates, during the roaming phase, they are more naïve to the landscape matrix they move through. Forest appeared, however, to be equally important in each phase. Being a prominent landscape feature, forest can be easily recognized in the distance during migratory trips through unknown landscapes, and actively selected for. The selection of locations closer to roads during the sedentary phase around Sarikamiş forest may be due to the presence of additional food resources deriving from intensive picnic activities (pers. observ.), but further investigation is necessary. Including not only nonlinear responses of distance to roads but also of distance to villages and elevation, could help further understand

the mechanisms of habitat selection. We caution for over interpretation of the results for the roaming and stopover phase due to the moderate model performance (see Appendix S3, for further considerations).

To summarize, we showed that the availability of a human-related source of food can cause a behavioral dichotomy among individuals of a confined population. This inter-individual variation is manifested in alternative feeding habits, movement pattern and selection of different habitat types. Therefore, identification and consideration of observed variation in behavioral types is fundamental for the correct implementation of evidence-based conservation strategies. Failures to detect such differences could result in the erroneous allocation of limited conservation resources, such as setting aside portions of land characterized by landscape features that are critical to only particular behavioral types (Simberloff *et al.*, 1992; Beier & Noss, 2008). Finally, because most research on brown bears has been carried out in northern Europe and North America, this work in Turkey increases our understanding of the species living under considerably different environmental, ecological and social conditions. Empirical evidence from this work thus adds valuable information for the implementation of management and conservation strategies of bears not only in Turkey but also worldwide.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Fieldwork and collection of GPS movement data.

Appendix S2. Net squared displacement.

Appendix S3. Step selection function.

Appendix S4. Observed movement paths.

Appendix S5. Vegetation differences between the Sarikamis forest and the stopover sites.