Animal Behaviour 183 (2022) 61–67

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Age Ain't Nothing But a Number: factors other than age shape brown bear movement patterns

Vincenzo Penteriani [a, *], Cindy Lamamy [a, b], Ilpo Kojola [c], Samuli Heikkinen [c], Cédric Vermeulen [b], María del Mar Delgado [a]

[a] Biodiversity Research Institute (IMIB, CSIC- University of Oviedo-Principality of Asturias), Campus Mieres, Mieres, Spain
[b] Forest Is Life, TERRA Research Unit, Gembloux Agro-Bio Tech, Université de Liège, Gembloux, Belgium
[c] LUKE, Natural Resources Institute, Rovaniemi, Finland

ARTICLE INFO

Article history:
Received 8 February 2021
Initial acceptance 25 March 2021
Final acceptance 4 October 2021

MS. number: 21-00098R

Keywords:
equifinality
home range
hyperphagia
mating
movement ecology
net distance
speed
Ursus arctos

Movement patterns may reflect individual age-specific variation. For example, individuals that sample novel areas (e.g. natal dispersal) may show different movements from those of adults settling in more stable areas and moving around local environments to procure food and shelter. The long-term study of a solitary large carnivore, the brown bear, *Ursus arctos*, allowed us to test for age-related differences in movement behaviour and, more specifically, for potential inter- versus intraindividual variation among adult versus subadult bears. In addition to age, we also explored factors other than individual characteristics that have the potential to determine movement patterns: sex, season (mating versus hyperphagia) and body weight. The contribution of age to movement patterns seemed to be irrelevant, most of the observed movement patterns being primarily explained by season and body weight. Moreover, intraindividual movements within a home range were more marked among subadult brown bears. We hypothesize that two mechanisms may lead to subadults and adults moving similarly. First, both must hibernate and, consequently, need to store energy during hyperphagia. Second, although triggered by different factors, both make erratic/long movements after hibernation, for dispersal (subadults) or mating (adults), which might contribute to shaping similar movement patterns. Different motivations could thus be expressed through the same behavioural patterns, and equifinality (i.e. similar ecological patterns emerge from different initial conditions) might be considered an intrinsic property of animal behaviours.

© 2021 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Animals differ in their expression of a variety of behaviours, and this can be due to a multitude of intrinsic factors, such as age, sex, size and internal state. In addition to differences in behaviour attributable to such factors, animals also exhibit consistent individual differences in behaviour for a wide range of traits, across time and contexts (Nilsson et al., 2014).

Movement is a central population process, and some important population phenomena depend on individual movement behaviour (Abrahms et al., 2020; Jingxuan & Jiang, 2020; Patterson et al., 2008). The needs and experience of animals change throughout life, and movement patterns should reflect this age-specific variation (Delgado et al., 2009; Delgado et al., 2010; Graf et al., 2016). For example, subadult individuals that actively sample novel areas for short periods, for example during natal dispersal, should show different movement behaviours from adults, which settle more permanently in an area (Delgado et al., 2009). The dispersal of juveniles is inherently riskier than remaining in a well-known area (Fletcher et al., 2019), which is typical of adults that generally move around local environments to procure food, find shelter and seek mating opportunities (Abrahms et al., 2020; Fletcher et al., 2019). Longer residence times than those that characterize areas crossed during dispersal and, consequently, more accurate spatial information allow an individual to reduce uncertainty about its position with respect to given locations and resources (Fagan et al., 2013). For example, individual differences in movement patterns related to age have been found in moose, *Alces alces*, with older males having larger home ranges than younger individuals (Cederlund & Sand, 1994), wild boars, *Sus scrofa* (Keuling et al., 2008), and Eurasian beavers, *Castor fiber* (Graf et al., 2016). Different extents of extraterritorial movement have also been observed between adult and yearling wolves, *Canis lupus* (Messier, 1985).

* Corresponding author.
E-mail address: v.penteriani@csic.es (V. Penteriani).

https://doi.org/10.1016/j.anbehav.2021.10.020
0003-3472/© 2021 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Dispersing individuals have a high risk of mortality (e.g. human-induced causes, resource deprivation, unfavourable environmental conditions; Bonte et al., 2012). Moreover, dispersing through some environments is more challenging than moving through others, leading to differences in movement patterns (Fletcher et al., 2019). Thus, analyses of animal movements that include the different stages that individuals go through over their lifetime, that is, from natal dispersal to adulthood and mating when individuals shift from a wandering to a more sedentary phase characterized by settlement in fairly fixed areas of activity (Delgado & Penteriani, 2008; Delgado et al., 2009), represent a unique opportunity to explore possible age-specific variation in movement patterns, one of the notable gaps in movement ecology (Nathan et al., 2008). Although many facets of animal movements have been extensively studied for a long time (Fagan et al., 2013; Fletcher et al., 2019; Nilsson et al., 2014), how important age is in driving animal movement is still an open question in movement ecology.

We studied a solitary large carnivore , the brown bear, *Ursus arctos*, a species with overlapping home ranges (Dahle & Swenson, 2003b). Individuals disperse from their natal home range as subadults (1–4 years old; Støen et al., 2006; Zedrosser et al., 2007). Although both females and males may disperse long distances (Shirane et al., 2019), females usually tend to disperse less often or over shorter distances than males (Støen et al., 2006). We examined a data series from a long-term study (12 years) of brown bears in southern and central Finland and Russian Karelia. Our main aim was to characterize and compare the movement behaviour of subadults versus adults. We further investigated the extent of individual variation with the aim of understanding whether inter-and intraindividual differences in movement behaviours depend on individual age. In particular, because adult brown bears tend to move short distances within well-established home ranges (e.g. for mating, Støen et al., 2006; Zedrosser et al., 2007), we predicted their interindividual variation would be higher than their intra-individual variation. Similarly, we also predicted that subadult individuals, which usually move across largely unknown surroundings and over large distances, might have higher intra- than interindividual variation. In addition to age, we predicted that other individual characteristics, such as sex, seasonal requirements (i.e. mating and hyperphagia) and/or physical characteristics (e.g. body weight) might also affect movements in (1) a nonmutually exclusive way or (2) in a more prevalent way than age, thus hindering the effect of age on movement patterns.

We hypothesized that three distinct scenarios are possible. First, owing to the diverse needs of individuals of different ages, movement patterns of subadult and adult bears may differ, with, for example, longer movements of subadults (Pop et al., 2018), as they are mainly influenced by natal dispersal. In the second scenario, age has less effect because of the requirements of a given season, for example longer movements over large areas during the mating season (Dahle & Swenson, 2003a, 2003b) or an increase in searching for food during the hyperphagia season (Penteriani & Melletti, 2021) because of physiological constraints during hibernation (González-Bernardo et al., 2020). Consequently, movement patterns will be mostly the result of different seasonal requirements rather than age. Finally, movement behaviour may be affected by interactions between intrinsic (e.g. age, sex, body size) and extrinsic (seasonal requirements of bears) factors (Kay et al., 2017).

METHODS

Data Collection

From 2002 to 2013, we captured and radio-collared 57 brown bears (Table 1) inhabiting southern and central Finland and Russian Karelia (for more details on the study area, see Penteriani et al., 2021). When captured (for more details on the capture protocol followed, see Penteriani et al., 2021), bears were sexed and weighed. Additionally, they were classified as subadults (1–4 years old) or adults (> 5 years old; Craighead et al., 1970, Støen et al., 2006; Zedrosser et al., 2007).

Bears were fitted with GPS transmitters (Televilt, Lindesberg, Sweden; Vectronic Airspace, Berlin, Germany; for more information see Penteriani et al., 2021) that collected one location every 2 h ($N = 74\,724$ locations excluding the denning period), corresponding to 28 789 locations for subadults and 45 935 locations for adults (mean number of locations per individual ± SD = 978.2 ± 957.2). The weight of the collars (ca. 600 g) was less than 1.0–2.0% of the body weight of adult females (mean ± SD = 124.6 ± 27.5 kg) and 0.5–1.0% of adult males (mean ± SD = 212 ± 61.4 kg). We recorded the positional dilution of precision value for all 3-D fixes and the horizontal dilution of precision for 2-D fixes. Because 2-D fixes have higher location error, we removed them following the method developed by D'Eon et al., (2002) to increase the accuracy of the data and therefore of the movement metrics. Although this data-screening method reduces the data set, it allows us to detect a high percentage of large location errors (Bjørneraas et al., 2010).

By using the package adehabitat, version 0.4.15, for R software (Calenge, 2006), we estimated the following movement parameters for each daily trajectory: (1) average daily speed; (2) mean net distance, i.e. mean distance travelled between the initial position and the final position on a daily scale; (3) total distance, which is the sum of the distance between successive relocations on the same daily trajectory; and (4) the size of the home range (km^2) at a daily scale per individual using the local convex hull (LoCoH) method (Getz et al., 2007; Getz & Wilmers, 2004). To construct the daily LoCoH, we used the fixed number of points procedure, such that we first subsampled those days with at least eight locations, and then selected $k = 7$ as the optimum value parameter for constructing the LoCoH with our data set (for more details of this method, see Getz et al., 2007). We considered the following explanatory variables: (1) age (excluding females with cubs; Gardner et al., 2014); (2) sex; (3) season, i.e. mating (Dahle & Swenson, 2003b; Spady et al., 2007) versus hyperphagia (Ordiz et al., 2017); and (4) body weight (kg).

Ethical Note

For subadults, collars had a preprogrammed drop-off mechanism with an average battery life of 1 year. Whenever the drop-off did not occur by the scheduled time owing to technical flaws, the bear was recaptured, and the collar was removed manually. All collars were removed before the end of the project in 2014. Permission to capture and manipulate bears was issued by the County Veterinarian of Oulu and the Regional State Administrative Agency of Lahti (Finland). This research adheres to the ASAB/ABS Guidelines for the use of animals in research. The capturing of bears met the guidelines issued by the Animal Care and Use Committee at the University of Oulu (OYEKT-6–99), and permits were provided by the provincial government of Oulu (OLH-01951/Ym-23). During bear captures and tracking no adverse effects of manipulations were observed.

Statistical Analyses

We studied whether and how subadult and adult brown bears differ in their movement behaviours taking sex, body weight and season into account. As the effect of sex may not necessarily be additive with body weight and age, we also included their interaction terms. We fitted linear mixed models (LMMs) with the four calculated movement parameters as response variables. Visual

Table 1
Characteristics of daily movement patterns of subadult (13 males and 9 females) and adult (25 males and 10 females) brown bears

	Subadults	Adults	Subadult males	Subadult females	Adult males	Adult females
Speed (m/s)	0.01 ± 0.08 (0.0–0.6; 2275)	0.1 ± 0.09 (0.0–1.0; 2560)	0.1 ± 0.1 (0.0–0.6; 882)	0.1 ± 0.1 (0.0–0.6; 1369)	0.1 ± 0.1 (0.0–1.0; 1829)	0.1 ± 0.1 (0.0–0.5; 755)
Mean net distance (m)	14 637 ± 13 338 (84–81 474; 2275)	33 645 ± 36 640 (241–155 548; 2560)	17 442 ± 15 710 (84–81 474; 882)	12 145 ± 9621 (157–56 354; 1369)	38 266 ± 39 718 (314–155 548; 1829)	23 087 ± 24 334 (241–88 588; 755)
Total distance (m)	9049 ± 7640 (20–136 851; 2275)	9819 ± 9830 (38–98 315; 2560)	9715 ± 8796 (20–136 851; 882)	8544 ± 6630 (20–73 902; 1369)	10 625 ± 11 108 (29–98 315; 1829)	7978 ± 5346 (38–40 907; 755)
Home range size (km^2)	4.5 ± 7.4 (0.02–85.9; 718)	5.1 ± 10.3 (0.02–133.3; 767)	3.8 ± 6.7 (0.02–85.9; 436)	5.7 ± 8.3 (0.02–41.0; 327)	3.5 ± 4.6 (0.02–133.3; 440)	6.4 ± 12.9 (0.02–133.3; 440)

Means are given ± SD, with range and number of locations per bear group in parentheses. $N = 55\,756$ locations for the total of 57 individuals.

inspection of the data and model residuals was performed for all models to check for model assumptions and the presence of outliers. After we log-transformed the speed and home range variables, the residuals for all response variables were normally distributed and we therefore fitted the models using a normal distribution. In each model, we included the autoregressive correlation structure AR(1) to take the fact that daily movement parameters were temporally autocorrelated into account. To account for repeated but unbalanced measurements within individuals, we included the individual as a random factor. The set of competing models was generated with all subsets of explanatory variables in the full model and then we employed model averaging on the 95% confidence set to derive values of the Akaike information criterion corrected for small sample size (AICc), ΔAICc, weighted AICc (*w*) and parameter coefficients of each explanatory variable using the full-model averaging approach. Following standard procedures, we calculated the weighted AICc for each candidate model (*wi*) as the probability of model *i* being the best-approximating model from the set of candidate models. We considered models with ΔAICc values lower than 2 as equally competitive. When there might be high model selection uncertainty, model averaging allows formal inference based on the entire set of models considered (Grueber et al., 2011; Symonds & Moussalli, 2011). LMMs were run using the lme4 package (Bates & Maechler, 2009), while multimodel inference and model averaging were run using the MuMIn package (Barton, 2018).

Finally, to assess interindividual variation in movement behaviours for both subadult and adult bears, we rebuilt the most parsimonious models selected above. We estimated the proportion of the variance explained by the random intercept effect, by accounting for the variance explained by the fixed effects (i.e. adjusted interindividual repeatability). We used the rptR package in R (Nakagawa & Schielzeth, 2013; Stoffel et al., 2017) to calculate interindividual repeatability values (*R*), standard errors, 95% confidence intervals (CI) and statistical significance of repeatability. All analyses were performed using R 3.5.0 (R Development Core Team, 2018).

RESULTS

Age was never included as an explanatory variable in the most parsimonious models analysing daily brown bear movement behaviour (Table 2), indicating that movement patterns and the area prospected by individuals did not differ between age classes (Fig. 1). Factors other than age did influence bear movement patterns, even if only slightly (see R^2 in Table 2). Season, sex and body weight affected daily movement parameters more than age (Table 2), supporting our third hypothesis. In particular, at the daily scale (see Table 2 for parameter estimates of the models): (1) individuals moved slightly faster, over larger distances and had larger home ranges during the mating season (speed: mean ± SD = 0.1 ± 0.06 m/s; total distance = 8.8 ± 6.4 km; home range = 6.0 ± 11.4 km^2) than during the hyperphagia season (speed = 0.08 ± 0.07 m/s; total distance = 7.3 ± 5.4 km; home range = 3.5 ± 5.7 km^2); (2) males moved slightly shorter net distances (4.1 ± 2.9 km) but travelled over larger total distances (8.1 ± 5.2 km) within a smaller home range (3.6 ± 5.9 km^2) than females (daily net distance = 5.5 ± 2.7 km; total distance = 7.8 ± 6.6 km; home range = 6.1 ± 11.4 km^2); and (3) the heaviest bears had the smallest daily home ranges (Table 2).

Interindividual variation in movement behaviours was moderate (*R*; Fig. 1), indicating that individuals mostly adopted flexible movement behaviour. For interindividual differences adjusted *R*s ranged from 12% to 33% of the variation in the movement parameters considered (Fig. 1). Notably, interindividual variation was very similar for both subadult and adult bears for all movement parameters, except home range. Variation among home ranges was substantially higher among subadults than adults (Fig. 1).

DISCUSSION

Age contributed little to the daily patterns of the four movement parameters of brown bears (i.e. average daily speed, mean net distance, total distance and home range size) that we analysed here. Conversely, season, sex and body weight explained most of the observed daily movement patterns. Moreover, interindividual movement variation within a home range was more marked among subadults.

Little information exists on the effect of age on animal movements and, more specifically, on brown bear movement patterns; however, in accordance with our results, Ballard et al. (1982) did not find any differences associated with age in the daily movements of southcentral Alaskan grizzly bears, *Ursus arctos horribilis*. Dahle and Swenson (2003a, 2003b) found that both male and oestrous female brown bears moved further in the mating season, probably because both sexes roamed to find mates; their movement patterns could not be explained by seasonal changes in food availability or increased foraging movements of oestrous females to replenish body reserves after cub rearing. Similarly, movement behaviour and home range size of brown bears differed between seasons in Pop et al.'s (2018) study, with males having larger territories during the hyperphagia season. Body size influences an individual's physiology and imposes morphological and ecological constraints (Swihart et al., 1988). Despite the scarce information available on the relationship between body mass and animal movements and home range size (Haskell et al., 2002; Swihart et al., 1988), body mass has already been shown to affect, for example, movement tortuosity in forest-dwelling didelphid marsupials (Vinı & Prevedello, 2010) and, more generally, the size of mammal home ranges (Swihart et al., 1988). This is the case for our larger brown bears, which had smaller home ranges than smaller individuals. Finally, even though we did not find any age-related difference in speed, as reported by Hernando et al. (2020) for a human-modified landscape in Greece, we detected similar patterns for the influence of the mating season on movement peaks. The activity rates and high home range variation recorded for subadult males in Greece (Hernando et al., 2020)

Table 2
Model selection table and model-averaged coefficients for movement patterns of subadult (13 males and 9 females) and adult (25 males and 10 females) brown bears

Dependent variable	Explanatory variables	Model-averaged coefficients			CI
		β	SE	*z*	
Speed (N=2619, R^2m=0.05; R^2c=0.09), competing model =season, *df*=5, AICc=-7925.53, ΔAICc=0.00, weight=0.97					
	Intercept	1.06e-01	0.77e-03	28.30	(7690.53; 12, 05.04)
	Season(hyperphagia)	-2.79e-02	3.82e-03	7.29	(1744.07; 268.95)
	Sex(male)	-2.66e-04	1.88e-03	0.14	(-7047.20, 1612.17)
	Body weight	5.61e-07	1.66e-04	0.003	(-2691.73; 308.94)
	Age(adult)	3.09e-06	4.25e-04	0.007	(-2940.05; 4595.09)
	Body weight*sex(male)	-2.93e-08	2.96e-05	0.001	(-7439.56; 3586.62)
	Age(adult)*sex(male)	1.15e-08	1.73e-05	0.001	(-4735.38; 4486.88)
Mean net distance (N=1045, R^2m=0.11; R^2c=0.37), competing model=Age*sex + Body weight*sex + Season, *df*=10, AICc=18 891.08, ΔAICc=0.00, weight=1.00					
	Intercept	4459.7	582.7	7.65	(3316.23; 5603.24)
	Body weight	-925.6	390.4	-2.37	(-1691.63; -159.55)
	Sex(male)	-253.4	1084.4	0.23	(2450.62; 1943.90)
	Season(hyperphagia)	251.7	246.00	1.02	(-230.31; 735.16)
	Body weight*sex(male)	-936.2	1428.7	0.65	(-3740.95; 1867.35)
	Age(adult)	515.6	959.6	0.54	(-1367.41; 2398.69)
	Age(adult)*sex(male)	515.1	1184.7	0.43	(-1809.98; 2841.14)
Total distance (N=1044, R^2m=0.02; R^2c= 0.23), competing model=Age*sex + Body weight*sex + Season, *df*=10, AICc=20 805.11, ΔAICc=0.00, weight=1.00					
	Intercept	9947.8	1150.3	8.64	(7690.54; 12 205.04)
	Season(hyperphagia)	-737.0	513.1	1.43.40	(-1744.07; 268.95)
	Body weight	-1191.4	764.6	1.55	(-2691.73; 308.94)
	Sex(male)	-2717.5	2136.9	1.23	(-7047.20; 1612.17)
	Age(adult)	827.5	1919.9	0.43	(-2940.05; 4595.09)
	Body weight*sex(male)	-1925.9	2809.2	0.68	(-7439.57; 3586.62)
	Age(adult)*sex(male)	-124.2	2349.3	0.05	(-4735.38; 4486.88)
Home range (N=1485, R^2m=0.04; R^2c=0.16), competing model=Season + Body weight, *df*=6, AICc=5258.95, ΔAICc=0.00, weight=0.27, competing model= Season, *df*=5, AICc=5260.26, ΔAICc=1.31, weight=0.14, competing model=Season + Body weight + Sex, *df*=7, AICc=5260.27, ΔAICc=1.31, weight=0.14					
	Intercept	0.75	0.18	4.16	(0.40; 1.11)
	Season(hyperphagia)	-0.32	0.16	1.96	(-0.61; -0.12)
	Body weight	-0.22	0.16	1.37	(-0.53; -0.06)
	Sex(male)	-0.11	0.23	0.44	(-0.88; 0.36)
	Age(adult)	0.05	0.17	0.27	(-0.41; 0.76)
	Body weight*sex(male)	0.04	0.19	0.19	(-0.64; 1.21)
	Age(adult)*sex(male)	-0.0008	0.11	0.008	(-1.01; 0.97)

N = 55 756 locations for the total of 57 individuals. For the explanatory variables, i.e. age, sex, body weight and season, we report the estimate (β), SE, *z*-value and confidence interval (CI) obtained from model-averaging coefficients on the 95% confidence set of models. Only the models with ΔAICc < 2 are shown.

has been considered the result of a mix of subadult inexperience in resource use and tolerance for humans, as well as an attempt to avoid intraspecific agonistic interactions. Because large home ranges for subadult males have also been recorded in other human-modified landscapes in Europe (Hernando et al., 2020), bear movement patterns might be a consequence of local differences in habitat quality or the perception of local risks, together with features of the landscape in which bears move.

Increases in distance moved and home range size may be the result of several nonmutually exclusive factors, for example (1) increased movement of males during the mating season to increase their rate of encounter with females (Dahle & Swenson, 2003b; Steyaert et al., 2012); (2) sexual size dimorphism (and, more generally, body size), which increases metabolic demands in males compared to females (or in larger individuals compared to smaller ones; Dahle & Swenson, 2003b); and (3) physiological needs during certain periods, such as the hyperphagia season, during which bears search for food in order to store fat reserves (González-Bernardo et al., 2020; Swenson et al., 2021). Note that although season was always included in the most parsimonious models for both individual movements and home ranges in our study, it generally had a weak effect. This may be because we assumed fixed dates for the seasons. As there may be interindividual and interannual variability in the dates, breaking the movement data into two discrete periods common to all individuals may have weakened the effect of season.

Our results might suggest that differences in age-related needs are not able to explain differences in movement patterns and home range size between subadults and adults (the first and third scenarios that we hypothesized). Thus, factors other than age might determine patterns of brown bear movement. For example, based on the parameters we analysed here, we can hypothesize that two mechanisms may lead to subadults and adults moving similarly. First, both must hibernate and, consequently, need to store energy during hyperphagia. As they have the same requirements, both adults and subadults may show similar food-oriented patterns of movement, that is, the common search for food determines the emergence of similar patterns of movement. Second, both adults and subadults move long distances after hibernation, but for different reasons. Both yearlings recently exited from winter dens with their mothers and older subadults are predicted to make erratic and long movements during their juvenile dispersal (Bonte et al., 2012; Clobert et al., 2001; Clobert et al., 2004; Zedrosser et al., 2007). The exploration of new areas in which to settle during dispersal might be one of the causes of the observed higher inter-individual variation in subadult movements. Because dispersal movements may occur anywhere during the exploration of new areas (Clobert et al., 2001; Delgado et al., 2009), subadults may cross diverse areas depending on their starting point after leaving the natal area. Interindividual variation in movement behaviour may be the result of individuals varying movement patterns and space use across gradients of, for example, food availability (Hertel, Niemelä et al., 2020; Hertel, Royauté et al., 2020; Webber et al., 2020). In contrast to subadults, adult brown bears move long distances to find mates (Dahle & Swenson, 2003b; Steyaert et al., 2012). Thus, after the spring den exit, both subadults and adults need to travel long distances, for dispersal and mating, respectively, and thus their movement patterns converge. That is, all individuals end up behaving (i.e. moving) similarly, regardless of the initial state or movement aims that drive convergence in behaviour (Luttbeg & Sih, 2010).

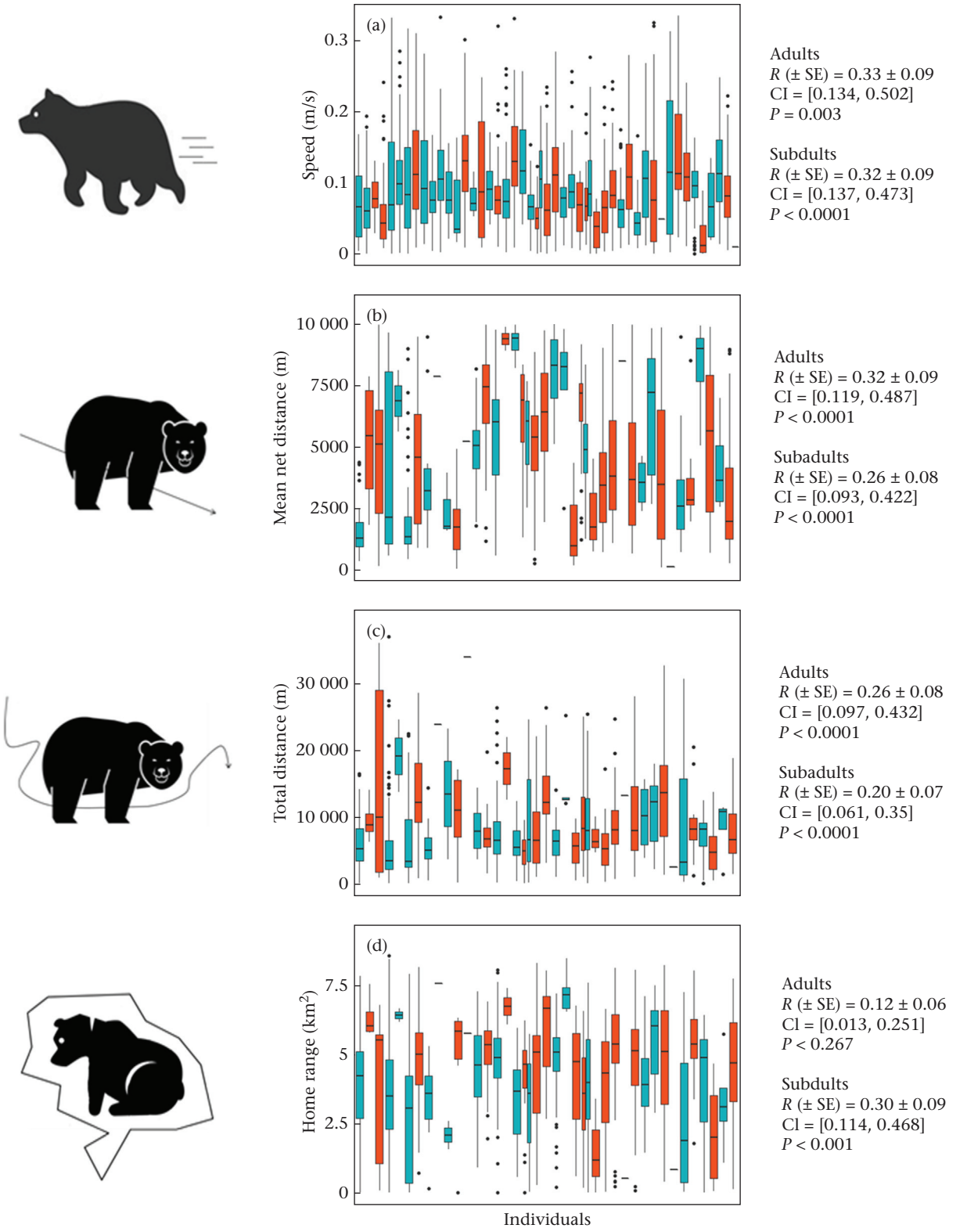

Figure 1. Adult (blue bars) versus subadult (orange bars) brown bear daily movement behaviours ($N_{subadults} = 2275$ localizations, $N_{adults} = 2560$ localizations): (a) speed (m/s); (b) mean net distance (m); (c) total distance (m); and (d) home range size (km^2). The edges of the box plots represent the interquartile range (IQR), the internal line is the median, the whiskers are the maximum (third quartile + 1.5×IQR) and the minimum (first quartile − 1.5×IQR) and the circles are outliers. For each movement parameter interindividual repeatability values (*R*), standard errors (SE), 95% confidence intervals (CI) and statistical significance of repeatability (*P*) are given. The icons were downloaded from 123RF royalty-free stock photos, http://www.123rf.com; speed: ID 89448738 vastard; mean net distance and total distance: ID36170731 Dejan Jovanovic; home range size: ID24965219 Khoon Lay Gan.

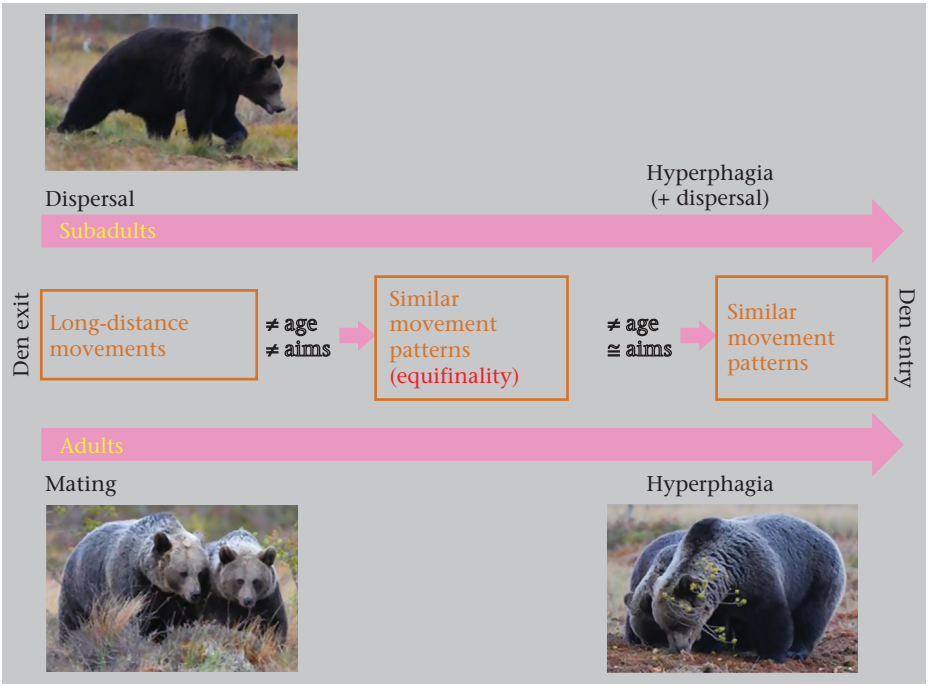

Figure 2. Different animal motivations may engender similar movement patterns which can lead to equifinality. In this summarized representation, from den exit after hibernation to den entry in order to hibernate, the main subadult and adult brown bear behaviours are shown: subadult dispersal and adult mating, which overlap temporally, and hyperphagia, which both adult and subadult bears experience. Long-distance movements occur during the subadults' explorations of new areas in which to settle (dispersal) and the mating period when adult bears search for mates. This is an example of equifinalistic behaviour, i.e. similar ecological patterns emerge from different initial conditions, which is represented here by the need for long displacements determined by both subadult dispersal and adult mating. See text for further details. Photo credit: V. Penteriani.

Equifinality occurs when similar ecological patterns emerge from different initial conditions (Penteriani, 2008). Thus, different motivations (subadult dispersal versus adult mating in our case) could be expressed through the same individual behaviour (Aspden et al., 2010) and equifinality (sensu von Bertalanffy, 1950) might be considered an intrinsic property of certain animal behaviours. The concept of equifinality can help explain why similar patterns have different origins: they can be the result of different causes, factors or pressures, such as the need for long movements determined by both subadult dispersal and adult mating (Fig. 2). That is, independent of their causes or stimuli, similar movement patterns may result from different behaviours (Popescu & Rymer, 2000). To our knowledge, this is the first time that equifinality has been detected in the movement patterns of a large carnivore and, more generally, in movement ecology. Our study shows how careful we need to be when examining behavioural patterns in animal populations, as equifinality may lead to mistakes in our understanding of the mechanisms behind observed patterns (von Bertalanffy, 1950).

Author Contributions

V.P. and I.K. conceived of the study; V.P., I.K., C.L. and M.M.D. designed the study; I.K. and S.H. administrated the study and collected the data; M.M.D., V.P. and C.L. analysed the data; V.P. drafted the manuscript; M.M.D., C.L., I.K., S.H. and C.V. critically revised the manuscript. V.P., I.K. and S.H. provided funding.

Acknowledgments

This work was supported by the I+D+i Project PID 2020-114181GB-I00 financed by the Spanish Ministry of Science and Innovation, the Agencia Estatal de Investigación (AEI) and the Fondo Europeo de Desarrollo Regional (FEDER, EU). M.M.D. was financially supported by the Spanish Ramon y Cajal grant RYC-2014-16263. The Ministry of Agriculture and Forestry financially supported I.K. We thank Antero Hakala, Leo Korhonen, Reima Ovaskainen, Seppo Ronkainen and Markus Suominen for assistance in capturing and collaring the bears. Two referees provided useful comments that improved the manuscript.

References

Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2020). Emerging perspectives on resource tracking and animal movement ecology. *Trends in Ecology & Evolution, 2777*, 1–13. https://doi.org/10.1016/j.tree.2020.10.018

Aspden, T., Ingledew, D., & Parkinson, J. (2010). Motives and health-related behaviours an investigation of equipotentiality and equifinality. *Journal of Health Psychology, 15*, 467–479. https://doi.org/10.1177/1359105309355333

Ballard, W. B., Miller, S. D., & Spraker, T. H. (1982). Home range, daily movements, and reproductive biology of Brown bears in southcentral Alaska. *Canadian Field-Naturalist, 96*, 1–5.

Barton, K. (2018). *Package 'MuMIn': Multi-model inference*. http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bates, D., & Maechler, M. (2009). *lme4: Linear Mixed-Effects Models using S4 Classes*. Version 0.999375-31 https://cran.r-project.org/web/packages/lme4/lme4.pdf.

Bjørneraas, K., Van Moorter, B., Rolandsen, C. M., & Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *Journal of Wildlife Management, 74*(6), 1361–1366. https://doi.org/10.2193/2009-405

Bonte, D., Dyck, H. Van, Bullock, J. M., Delgado, M., Gibbs, M., Lehouck, V., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews, 87*, 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Calenge, C. (2006). The package 'adehabitat' for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling, 197*(3–4), 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Cederlund, G., & Sand, H. (1994). Home-range size in relation to age and sex in moose. *Journal of Mammalogy, 75*, 1005–1012.

Clobert, J., Danchin, E., Dhondt, A., & Nichols, J. (2001). *Dispersal*. Oxford University Press.

Clobert, J., Ims, R., & Rousset, F. (2004). Causes, mechanisms and consequences of dispersal. In I. Hanski, & O. Gaggiotti (Eds.), *Ecology, genetics, and evolution of metapopulations* (pp. 307–335). Academic Press.

Craighead, J. J., Craighead, F. C., & McCutchen, H. E. (1970). Age determination of grizzly bears from fourth premolar tooth sections. *Journal of Wildlife Management, 34*(2), 353. https://doi.org/10.2307/3799022

Dahle, B., & Swenson, J. (2003a). Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology, 72*, 660–667.
Dahle, B., & Swenson, J. E. (2003b). Home ranges in adult scandinavian brown bears (*Ursus arctos*): Effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology, 260*, 329–335. https://doi.org/10.1017/S0952836903003753
Delgado, M. D. M., & Penteriani, V. (2008). Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. *The American Naturalist, 172*(4). https://doi.org/10.1086/590964
Delgado, M. M., Penteriani, V., Nams, V. O., & Campioni, L. (2009). Changes of movement patterns from early dispersal to settlement. *Behavioral Ecology and Sociobiology, 64*(1). https://doi.org/10.1007/s00265-009-0815-5
Delgado, M., Penteriani, V., Revilla, E., & Nams, V. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology, 79*(3), 620–632. https://doi.org/10.1111/j.1365-2656.2009.01655.x
D'Eon, R. G., Serrouya, R., Smith, G., & Kochanny, C. O. (2002). GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin (1973-2006), 30*(2), 430–439.
Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., … Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters, 16*, 1316–1329. https://doi.org/10.1111/ele.12165
Fletcher, R. J., Sefair, J., Wang, C., Poli, C. L., Smith, T. A. H., Bruna, E. M., … Acevedo, M. (2019). Towards a unified framework for connectivity that disentangles movement and mortality in space and time. *Ecology Letters, 22*, 1680–1689. https://doi.org/10.1111/ele.13333
Gardner, C. L., Pamperin, N. J., Benson, J. F., Gardner, C. L., Pamperin, N. J., & Benson, J. F. (2014). Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska. *Ursus, 25*(2), 121–138. https://doi.org/10.2192/URSUS-D-14-00015.1
Getz, W., Fortmann-Roe, S., Cross, P., Lyons, A., Ryan, S., & Wilmers, C. (2007). LoCoH: Nonparameteric kernel methods for constructing home ranges and utilization distributions. *PLoS One, 2*, Article e207.
Getz, W., & Wilmers, C. (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography, 27*, 489–505.
González-Bernardo, E., Russo, L., Valderrábano, E., Fernández-González, A., & Penteriani, V. (2020). Denning in brown bears. *Ecology and Evolution, 10*, 6844–6862.
Graf, P. M., Mayer, M., Zedrosser, A., Hackländer, K., & Rosell, F. (2016). Territory size and age explain movement patterns in the Eurasian beaver. *Mammalian Biology, 81*(6), 587–594. https://doi.org/10.1016/j.mambio.2016.07.046
Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology, 24*, 699–711.
Haskell, J. P., Ritchie, M. E., & Olff, H. (2002). Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature, 418*, 527–530.
Hernando, M. D. G., Karamanlidis, A. A., Papakostas, G., & Beecham, J. (2020). Reduced movement of wildlife in mediterranean landscapes : A case study of brown bears in Greece. *Journal of Zoology*. https://doi.org/10.1111/jzo.12768
Hertel, A. G., Hertel, A. G., Niemelä, P. T., Dingemanse, N. J., Mueller, T., & Mueller, T. (2020). A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecology, 8*, 30. https://doi.org/10.1186/s40462-020-00216-8
Hertel, A. G., Royauté, R., Zedrosser, A., & Mueller, T. (2020). Biologging reveals individual variation in behavioural predictability in the wild. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.13406
Jingxuan, W., & Jiang, G. (2020). Advances in terrestrial mammal movement ecology: An overview. *Journal of Zoological Research, 1*(2), 28–35. https://doi.org/10.30564/jzr.v1i2.1717
Kay, S. L., Fischer, J. W., Monaghan, A. J., Beasley, J. C., Boughton, R., Campbell, T. A., … Pepin, K. M. (2017). Quantifying drivers of wild pig movement across multiple spatial and temporal scales. *Movement Ecology, 5*, 14. https://doi.org/10.1186/s40462-017-0105-1
Keuling, O., Stier, N., & Roth, M. (2008). Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *European Journal of Wildlife Research, 54*(3), 403–412. https://doi.org/10.1007/s10344-007-0157-4
Luttbeg, B., & Sih, A. (2010). Risk , resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B, 365*, 3977–3990. https://doi.org/10.1098/rstb.2010.0207
Messier, F. (1985). Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Canadian Journal of Zoology, 63*, 239–245.
Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*, 133–142.
Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences, 105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105
Nilsson, J.-åke, Brönmark, C., Hansson, L., & Chapman, B. B. (2014). Individuality in movement : The role of animal personality. In L.-A. Hansson, & S. Åkesson (Eds.), *Animal movement across scales* (pp. 90–109). Oxford University Press.
Ordiz, A., Saebø, S., Kindberg, J., Swenson, J. E., & Støen, O.-G. (2017). Seasonality and human disturbance alter brown bear activity patterns: Implications for circumpolar carnivore conservation? *Animal Conservation, 20*(1), 51–60. https://doi.org/10.1111/acv.12284
Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State – space models of individual animal movement. *Trends in Ecology & Evolution, 23*, 87–94. https://doi.org/10.1016/j.tree.2007.10.009
Penteriani, V. (2008). When similar ecological patterns in time emerge from different initial conditions : Equifinality in the breeding performance of animal populations. *Ecological Complexity, 5*, 66–68. https://doi.org/10.1016/j.ecocom.2007.06.002
Penteriani, V., Lamamy, C., Kojola, I., Heikkinen, S., Bombieri, G., & Delgado, M. (2021). Does artificial feeding affect large carnivore behaviours ? The case study of brown bears in a hunted and tourist exploited subpopulation. *Biological Conservation, 254*, 108949. https://doi.org/10.1016/j.biocon.2021.108949
Penteriani, V., & Melletti, M. (2021). *Bears of the world: Ecology, conservation and management*. Cambridge University Press.
Popescu, F. C., & Rymer, W. Z. (2000). End points of planar reaching movements are disrupted by small force pulses: An evaluation of the hypothesis of equifinality. *Journal of Neurophisiology, 84*, 2670–2679.
Pop, M. I., Iosif, R., Miu, I. V., & Rozylowicz, L. (2018). Combining resource selection functions and home-range data to identify habitat conservation priorities for brown bears. *Animal Conservation, 21*, 352–362. https://doi.org/10.1111/acv.12399
R Development Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/.
Shirane, Y., Shimozuru, M., Yamanaka, M., Tsuruga, H., Nakanishi, M., Ishinazaka, T., … Masuda, Y. (2019). Sex-biased dispersal and inbreeding avoidance in Hokkaido brown bears. *Journal of Mammalogy, 100*(4), 1317–1326. https://doi.org/10.1093/jmammal/gyz097
Spady, T. J., Lindburg, D. G., & Durrant, B. S. (2007). Evolution of reproductive seasonality in bears. *Mammal Review, 37*(1), 21–53. https://doi.org/10.1111/j.1365-2907.2007.00096.x
Steyaert, S. M. J. G., Endrestøl, A., Hackländer, K., Swenson, J. E., & Zedrosser, A. (2012). The mating system of the brown bear *Ursus arctos*. *Mammal Review, 42*(1), 12–34. https://doi.org/10.1111/j.1365-2907.2011.00184.x
Støen, O.-G., Zedrosser, A., Sæbø, S., & Swenson, J. E. (2006). Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia, 148*, 356–364.
Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution, 8*(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797
Swenson, J. E., Ambarlı̄, H., Arnemo, J. M., Baskin, L., Danilov, P. I., Delibes, M., … Steyaert, S. M. J. G. (2021). Brown bear (*Ursus arctos* Linnaeus, 1758). In V. Penteriani, & M. Melletti (Eds.), *Bears of the world: Ecology, conservation and management* (pp. 139–161). Cambridge University Press.
Swihart, R. K., Slade, N. A., & Bergstrom, B. J. (1988). Relating body size to the rate of home range use in mammals. *Ecology, 69*, 393–399.
Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology, 65*, 13–21.
Vını, M., & Prevedello, J. A. (2010). Movement behaviour within and beyond perceptual ranges in three small mammals : Effects of matrix type and body mass. *Journal of Animal Ecology, 79*, 1315–1323. https://doi.org/10.1111/j.1365-2656.2010.01736.x
von Bertalanffy, L. (1950). The theory of open systems in physics and biology. *Science, 111*, 23–29.
Webber, Q. M. R., Laforge, M. P., Bonar, M., Robitaille, A. L., Hart, C., Zabihi-Seissan, S., & Wal, E. Vander. (2020). The ecology of individual differences empirically applied to space-use and movement tactics. *The American Naturalist, 196*(1), E1–E15. https://doi.org/10.1086/708721
Zedrosser, A., Støen, O. G., Sæbø, S., & Swenson, J. E. (2007). Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour, 74*(3), 369–376. https://doi.org/10.1016/j.anbehav.2006.09.015