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Modelling activity patterns of wild animals - An application of the multiple discrete-continuous extreme value (MDCEV) model

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ABSTRACT

Advanced econometric models used in the field of transport or marketing are becoming increasingly sophisticated and able to capture complex decision making and outcomes. In this paper, we apply state-of-the-art discrete-continuous choice models to the field of Ecology, in particular to model activity engagement of the population of Swedish Brown bears. Using data from GPS collars that track wild animals over time, we estimate a Multiple Discrete-Continuous Extreme Value (MDCEV) model to understand activity engagement and duration as a function of both bear characteristics and other external factors. We show that the methodology is not only suitable to address this aim, but also allows us to produce insights into the connection between the animal's age and gender and activity engagement as well as the links with climate variables (temperature and precipitation) and human activity (hunting).

1. Introduction

The understanding of the patterns of movement of living organisms is a prominent area of study in animal biology and ecology. Indeed, the presence and distribution of different animals in space and time are a product of the underlying process of animal movement (Turchin, 1998; Nathan et al., 2008; Kays et al., 2015). Identifying behavioural states along an animal's movement path is straightforward when visual observation is possible (Bates and Byrne 2009; Hayward et al., 2009). Direct observation is an effective method for investigating animal behaviour and the least prone to errors when it comes to identifying the specific behavioural state (Loettker et al., 2009; Shamoun-Baranes et al., 2012). However, in most cases it is challenging if not impossible to constantly observe animals as they go through their lives in their natural habitat. Wild animals are often elusive and can reside in remote areas with challenging terrain. Many species minimize exposure to perceived threats, which often include human encroachments. Due to the difficulties in locating and observing animals, early studies have been marred by small sample sizes, often resulting in insufficient data for statistical inference (Caro 2007). In addition, investigating wild animal behaviour via direct observation may pose threats to researcher safety.

The development and diffusion of animal telemetry devices has revolutionized the ability to study animal movements and behaviour in the wild (Cagnacci et al., 2010; Kays et al., 2015), helping to overcome many of the practical, logistical, and financial challenges of direct field observation. Recent advances in GPS radiocollar technologies allow tracking of animals for long sampling periods, providing large data sets of locations at flexible time intervals (Cagnacci et al., 2010). Telemetry data have created possibilities that allow to address some of the most fundamental ecological hypotheses about space use, movement, resource selection and behaviour. The GPS locations can be used to investigate, among others, habitat selection (Signer et al., 2019), spatiotemporal

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movements (Nathan et al., 2008) and habitat influences on animal movement (Patterson et al., 2008). One line of research specifically relevant to the present work is the use of GPS radio-collar data to infer and analyse animal behavioural states. A common assumption in the ecology literature is that individual animals have a small set of movement strategies (Nathan et al., 2008), and the time allocation to different behaviours (or "activity budgets") depends on environmental, individual animals' characteristics and external factors (Hooten et al., 2017). There are many approaches to infer animals' behaviour from radio-collar data. Some studies have decomposed an individual animal's movement trajectory into a broad set of movement bouts based on rates of movement (Johnson et al., 2002). Others have inferred behavioural states based on the time required for an animal to first move out of a circle centred on a location along their path (Frair et al., 2005) or total time spent in the vicinity of a location (Barraquand and Benhamou 2008). For example, in carnivore studies in which authors attempt to derive behaviour from GPS relocation data, the main goal has often been to identify GPS location clusters indicative of predation or bedding events (Merrill et al., 2010; Ordiz et al., 2011; Rauset et al., 2012). Clusters form when an animal spends a certain amount of time within a site of a given radius, where time and radius are specified by the researcher and should be tailored to the behaviour of the study species and field conditions.

Movement trajectory and cluster analysis are common techniques for identifying behavioural states, such as resting (Ordiz et al., 2011), predation (Rauset et al., 2012) or foraging (Bastille-Rousseau et al., 2011; Hertel et al. 2016a, 2016b). Frequently used methodologies to study patterns of animal movement and behaviour are autocorrelation analysis (Boyce et al., 2010) or generalized additive models for either net squared displacement or step length (Ciuti et al., 2012). The detailed overview of these techniques can be found in (Gurarie et al., 2016; Hooten et al., 2017). Simple random-utility based models (such as logit models) have also been used to study the behavioural states (e.g. Ordiz et al., 2011).

While the above-mentioned studies provide interesting insights into animal behavioural states, they are generally narrow in scope because they focus on the analysis of a single type of behaviour (also referred to as "activity" from here on) in isolation. This can limit the insights produced due to the lack of the overall picture: for example, an animal could move in a given direction so that they can conduct another activity, or because they have been conducting another activity/experienced certain circumstance.

The present work represents an advancement in this field of research not only by analysing engagement in multiple activities within a given time frame, but by jointly modelling activity choice and its duration. We refer to such choice processes as discrete-continuous. Many studies involving humans have recognised the importance of accommodating for the joint nature of multiple discrete-continuous decisions in econometric models (e.g. Bhat, 2005; Calastri et al., 2022; Van Nostrand et al., 2013). In this work we aim to test whether models accounting for the discrete-continuous nature of activity choice can be used to infer more detailed insights about animals' behaviour by acknowledging the connection between the choice of activity and its duration. For example, an important topic in brown bear research, highly relevant from the management and conservation perspective, is the impact of hunting on bears behaviour. A few studies have demonstrated that apex predators may perceive and respond to human-caused risk like prey responds to a natural predator (Ordiz et al., 2011). However, these studies explore the impact of hunting on a single behavioural state, for example Hertel et al. (2016a) analysed the impact of hunting on foraging, Ordiz et al. (2011) analysed the impact of hunting on the choice of places for bedding, whereas in this work we are able to document the impact of hunting on engagement in multiple activities and their durations. Our approach allows for better understanding of the full cost in terms of energy expenditure and intake for bears resulting from hunting. These topics lay in the heart of budget activity (Christiansen et al., 2013) and foraging ecology (Pyke, 2019).

Multiple discrete-continuous models have not been previously applied in Ecology, and this paper aims to present a proof-of-concept of their potential usefulness in this discipline.

In particular, by combining movement trajectory and cluster analysis we identify distinct behavioural states of brown bears (*Ursus arctos*) (i.e., rest, forage, move). We then apply the state-of-the-art Multiple Discrete-Continuous Extreme Value (MDCEV) model to jointly represent the engagement in and duration of activities. The long-term individual-animal based dataset used in this study allows us to better understand the effect of individual bear characteristics, environmental variables and external factors on bear behaviour over time.

The remainder of this paper is organised as follows. The next section presents the data, before we discuss the model structure. This is followed by the results of the empirical analysis, and finally, the study conclusions.

2. Methods

2.1. Species description, study area and data collection

The GPS telemetry data from brown bears are collected as part of the Scandinavian Brown Bear Research Project (www.bearproject.info), an individual-bear level, long-term population monitoring program in south-central Sweden. The bear population in the study area has been continuously monitored since 1985 (Swenson et al., 1994). As part of this project, bears are captured by darting (Dan-Inject, Børkop, Denmark) with an immobilizing drug from a helicopter soon after hibernation and den emergence in late April. Captured bears are equipped with a GPS collar (GPS Plus; Vectronic Aerospace, Germany) prior to re-release. For more information on capture and handling procedures, see Arnemo and Evans (2017).

The study area is situated in Dalarna and Gävleborg counties in south-central Sweden. The terrain is hilly, with elevations between 250 and 650m above sea level and mostly covered by intensively managed coniferous forests mainly composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and birch (*Betula* spp.). The human settlement in the area consist of 24 scattered small villages and a few seasonally used independent houses. Human population density is low and ranges from 4.1 to 7.1 habitants per km^2 (Ordiz et al., 2012), but there is an extensive network of forestry roads (Frank et al., 2015). Bear density is about 30 bears per 1,000 km^2 (Bellemain et al., 2005), and bears are hunted in the study area (Frank et al., 2017). The annual brown bear hunting season in Sweden starts on 21 August and lasts for approximately 2 months or until predefined quotas are filled. Hunting is allowed from 1h after sunrise until 2h before sunset (Bischof et al. 2008, 2018).

In this study, we have focussed on GPS relocation data from adult (≥4years) bears (Zedrosser et al., 2006, 2009) collected on an hourly basis between 2008 and 2015. We removed GPS locations with a dilution of precision >10[1] from the data (D'eon and Delparte 2005). We focussed our analysis on the *berry season* (15th July – 15th September) (Ordiz et al., 2011; Hertel et al., 2018), i.e., the time period when bears build adipose tissue reserves in preparation for hibernation (Manchi and Swenson 2005). During this time period, the bears in our study area forage almost exclusively on berries, mainly *Vaccinium* spp. (Stenset et al., 2016). As the main purpose of this paper is to showcase MDCEV modelling framework in ecology, to reduce ecological complexity, we focused on solitary adult males (n = 24) and adult females (n = 40). Low satellite coverage may lead to failed GPS fixes (Moe et al., 2007). In only 30.9% of days for which fixes were recorded, all 24 fixes were available. In order to preserve data quality, we resorted to retaining observations (at the day level) for which at least 22 hourly fixes had been recorded (50.8% of all days). While data with up to two discontinuous missing fixes were retained, if the two missing fixes were contiguous, the whole day of data was discarded. In the case of such discontinuous missing fixes, the position for the missing hour was approximated as the midpoint between the two nearest available relocations.

2.2. Behavioural classifications

Bear behaviour was classified into three activities based on GPS data: *foraging*, *resting*, and *moving*. The classification of the behavioural states was based on the existing literature for brown bears in the study area (i.e. Moe et al., 2007; Ordiz et al., 2011; Hertel et al., 2016a; Hertel et al., 2016b). A bear was defined as exhibiting resting behaviour when a minimum of three consecutive GPS locations within a radius of 30m were recorded based on 30-min GPS-relocation data (Ordiz et al., 2011). Given the coarser temporal resolution in our data (60 min time intervals), we defined resting behaviour (*Rest*) as an activity in which an animal stayed at least 1 h within a radius of 30m. Berry foraging by bears is characterized by slow and meandering movements (Stelmock and Dean, 1986). Hertel et al. (2016a, 2016b) defined berry foraging in our study population as continuous movements in which a bear covered a distance of 25–300 m over at least three consecutive 30 min intervals. Field validation by Hertel et al. (2016a) confirmed that bears were foraging on berries at 80% of the locations classified as forage based on GPS-relocation data. For the purposes of this study, we slightly modified the criterion used by Hertel et al. (2018) and defined feeding behaviour (*Feed*) as relocations within a distance of 30–300 m in 60 min (2 consecutive GPS fixes). Any behaviour with movements longer than 300 m in 60min was classified as *Move*. This resulted in a very wide range of travelled distances in this category (i.e., mean = 911 m, std dev = 592, max distance = 8,504m). Given the temporal resolution of our data, very heterogenous behaviour is likely within a 60 min interval, including the whole spectrum from mostly feeding to pure travel. We tested two approaches to deal with the *Move* category; first, we classified all observations with travelled distances longer than 300 m/h as *Move*; second, we further divided *Move* into two subcategories, *Short move* – including all relocations ranging between 300 m/h and 600 m/h, and *Move* comprising all relocations for which the covered distance was larger than 600m. The second approach resulted in significantly better model performance and was used in the final model specification.

Table 1 presents a summary of the sample characteristics based on the defined criteria. As can be seen, all four types of activities are conducted on the vast majority of all days, with *Rest* being conducted every day.

3. Modelling framework

3.1. Overview

The family of Multiple Discrete-Continuous Extreme Value (MDCEV) models initially developed by Bhat (2005) and subsequently extended in different directions (Bhat, 2008; Castro et al., 2012; Pinjari and Bhat, 2010; Mondal and Bhat, 2021; Palma and Hess, 2022), represents the current state of the art in modelling multiple discrete-continuous choices. Human travel behaviour has been the main field of application of this modelling framework, for example in the study of the choice of vehicle type and mileage (Bhat and Sen, 2006), and to type and duration of activities (Bhat, 2005; Calastri et al., 2022). Application beyond transport choices include those analysing residential energy consumption (Iraganaboina and Eluru, 2021), social interactions (Calastri et al., 2017) and consumer purchase behaviour (Lu et al., 2017). To the best of our knowledge, MDCEV has never been applied to the study of animal behaviour.

The model is derived coherently with the random utility maximisation theory in economics, but relaxes the mutual exclusivity assumption inherent in traditional discrete choice models. This means that subjects are not constrained to selecting one option (in our case one activity) but allocate their available resources to a combination of these. While the model has been developed in the generic context of consumption choices, we describe it in terms of time allocation decisions, in line with the application presented in this paper.

The MDCEV model is based on a direct utility function $U(x)$ that individuals (in this case bears) maximise by choosing to allocate a vector x of non-negative time intervals to each of the K possible activities, $x = (x_1, \ldots, x_K)$. The choice of total time allocation is subject to a time "budget" constraint $\sum x = E$, where E is the total time available.

The vector x generally includes a so-called "outside activity" to represent allocation to an activity that is always undertaken by all the individuals (bears) in the sample, in our case *Rest*. A decision needs to be made on the unit of measurement. In our case we work

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[1] Dilution of precision (DOP) is a term used in satellite navigation and geomatics engineering to specify the error propagation as a mathematical effect of navigation satellite geometry on positional measurement precision. Observations with DOP larger than 10 are considered as having too large error to be used for analysis (D'eon and Delparte 2005).

Table 1
Summary statistics of GPS relocation data of radio-collared brown bears during the berry season (15th July – 15th September) in south-central Sweden, 2008–2016.

Daily activity duration (hours)				
	Mean	*Std. dev.*	*Min.*	*Max.*
Rest	8.72	2.57	2	21
Feed	6.00	2.81	0	18
Short move	5.47	3.02	0	18
Move	3.79	2.06	0	11
Bear characteristics				
	Mean	*Std. dev.*	*Min.*	*Max.*
Sex	40 – females 24 – males			
Age (years, average in sample)	9.36	4.32	5	22
Number of observations (days) (% of the sample)				
July (15th – 30)	1,321 (28%)			
August (1st – 31)	2,399 (51%)			
Sept (1st – 15th)	967 (21%)			
Days with Rest > 0h	4,687 (100%)			
Days with Feed >0h	4,647 (99.1%)			
Days with Short move>0h	4,508 (96.2%)			
Days with Move>0	4,505 (96.1%)			
Total number of observations and number of observations per individual				
	Mean	*Std. dev.*	*Min.*	*Max.*
Number of obs (days) per bear	73.25	60.36	1	266
Total number of observations	4,687			

with data at the day level, implying a time budget of 24 h per observation. The time budget takes the following form:

$$\sum_{k=1}^{K} x = E, x_1 > 0, x_k \geq 0 \forall k \; (k = 2, \ldots K) \tag{1}$$

where in our model activity 1 is *Rest*, i.e. the *outside activity*, and K = 4 (Rest, Feed, Move and Short move) and E = 24 h.

3.2. Econometrics

The utility formulation, introduced by Bhat (2008) is given by:

$$U(x) = \frac{1}{\alpha_1}\psi_1 {x_1}^{\alpha_1} + \sum_{k=2}^{K} \frac{\gamma_k}{\alpha_k}\psi_k\left(\left(\frac{x_k}{\gamma_k}+1\right)^{\alpha_k} - 1\right), \tag{2}$$

such that $U(x)$ is quasi-concave, increasing and continuously differentiable with respect to x and ψ. ψ_k is the baseline utility accrued from activity k. It is a function of observed characteristics of the individual (bear) and of activity k, z_k, which also includes a constant δ_k representing the generic preference for activity k, so that $\psi_k = \psi_k(z_k) * e^{\varepsilon_k}$. The parameters γ_k and α_k relate to activity k. The γ_k parameters are translation parameters that allow the model to accommodate corner solutions, i.e. observations for which no time is allocated to a given activity k. They also affect satiation, as a higher γ_k implies that more time invested in the corresponding activity (x_k) is needed to reach saturation. The α_k parameter is solely associated with the satiation effect, i.e., decreasing marginal utilities.

Empirical identification requires some constraints for normalisation, and in our work, we make use of the implementation of the MDCEV model in which we have product-specific γ parameters, i.e. we estimate γ_k parameters for $k = 2,3,4$, along with a generic satiation parameter α. As in most of the work in the literature, all the model specifications that we estimated displayed an extremely small value of α for which we could not reject the null hypothesis that it was equal to zero, where, with $\alpha \to 0$, the utility form collapses to a log utility formulation (cf. Bhat, 2008) with:

$$U(x) = \psi_1 \ln(x_1) + \sum_{k=2}^{K} \gamma_k \psi_k \left(\frac{x_k}{\gamma_k} + 1\right) \tag{3}$$

This formulation implies that direct utility increases with additional units of consumption in a logarithmic fashion, i.e. with diminishing returns. The only parameters relating to satiation that we estimate are the γ_k terms, which can be interpreted in terms of how long the activities of *Feed*, *Move* and *Short move* are performed for.

The probability that an individual (bear) chooses a specific vector of time allocations $x_1{}^*, x_2{}^*, \ldots, x_M{}^*, 0, \ldots, 0$, where M of the K activities are performed in a given day, is given by:

$$P\left(x_1^*, x_2^*, \ldots, x_M^*, 0, \ldots, 0\right) = \frac{1}{p_1}\frac{1}{\sigma^{M-1}}\left(\prod_{m=1}^{M} f_m\right)\left(\sum_{m=1}^{M}\frac{p_m}{f_m}\right)\left(\frac{\prod_{m=1}^{M} e^{V_i/\sigma}}{\left(\sum_{k=1}^{K} e^{V_k/\sigma}\right)^M}\right)(M-1)!, \tag{4}$$

where σ is an estimated scale parameter and where $f_m = \left(\frac{1-\alpha}{x_m^*+\gamma_m}\right)$.

3.3. Specification for our study

3.3.1. The discrete choice

As mentioned above, the baseline utility ψ_k broadly captures the "discrete choice", i.e., the likelihood of performing an activity. In the present study, this is composed of a constant δ_k and additive shifts for each of the covariates we consider. Differently from discrete choice models, the δ constants in the MDCEV model are influenced by both the discrete and the continuous parts of the model, and this explains the fact that the values for the constants for the non-base activities can be positive even though the base alternative (*Rest*) is conducted more often.

3.3.2. The continuous choice

Analogously, in the case of the satiation component, we estimate one γ_k for each activity but allow for heterogeneity as a function of covariates, i.e., measuring the impact of the covariates on the continuous choice. Differently from the case of the baseline utility, the parameterisation of γ_k was operationalised in a multiplicative fashion. For example, the overall satiation from activity k was expressed as:

$$\gamma_k = \gamma_{k,base} * \prod_{i=1}^{I} f_k(z_i) \tag{5}$$

where $\gamma_{k,base}$ is a constant for activity k (reported as "Core parameters" in Table 3), z_i is one of a set of I covariates. For categorical variables, such as sex, we set a base category, and estimate a multiplier for others, meaning that for a covariate with L levels, we use $f_k(z_i) = \sum_{l=1}^{L}\kappa_{ikl} \cdot (z_i = = l)$, where $(z_i == l)$ is equal to 1 if z_i takes the l^{th} level, and zero otherwise, and where we fix $\kappa_{ikl} = 1$ for one category. For continuous variables, we use $f(z_i) = \left(z_i/\overline{z_i}\right)^{\lambda_{ik}}$, where the estimate of λ_{ik} captures the non-linearity.

We retained those effects in the model where the κ_{ikl} multipliers are significantly different from 1, or where the elasticity parameters λ_{ik} were different from 0, implying that $f(z_i)$ is different from 1.

3.3.3. Explanatory variables

In our MDCEV application, we have tested the effect of a range of variables that have been demonstrated by a large amount of ecological literature to be related to brown bears' behaviour. These mainly relate to environmental/climatic factors, characteristics of the animal and potential human impacts. Here and in the Results section, we only describe the variables for which statistically significant effects on activity choice and duration were found. These include the bears age, sex, and two climatic variables. The full list of the variables used in the final model specification is reported in Table 2.

Table 2
Explanatory variables used in the model.

Variable	Type of variable	Description
Sex	Categorical	1 = Solitary adult female 0 = Solitary adult male
Age	Categorical	1 = 4–8 years old 2 = 9–15 years old 3 = Older than 15
Average daily temperature	Continuous	Range: 4.63–22.1 °C Mean: 13.12 °C
Average daily precipitation	Continuous	Range: 0–33.47 mm Mean: 2.94 mm
Daily duration of daylight[a]	Continuous	Range: 12.89–18.36 h Mean: 15.73 h
Daily duration of twilight[a]	Continuous	Range: 3.24–7.23 h Mean: 4.86 h
Daily duration of night[a]	Continuous	Range: 0–7.86 h Mean: 3.40 h
Hunting season	Categorical	1 = hunting season 0 = not hunting season

[a] Calculated for the central location of our study area (Tackåsen, Sweden: 61.5N, 15.05E).

Table 3
Model results.

	Coefficient	Estimate	Rob. t-ratio (0)	Rob. t-ratio(1)
Baseline parameters	α	0 (fixed)	NA	NA
	γ *feed*	4.099	15.174	11.472
	γ *move*	7.062	12.609	10.824
	γ *short move*	4.107	19.403	14.679
	δ *feed*	0.668	2.289	−1.135
	δ *move*	−2.568	−9.067	−12.598
	δ *short move*	−2.175	−17.939	−26.186
Shifts in the δ parameters	Age 16+ *feed*	0.081	2.729	−30.781
	Age 16+ *move*	−0.361	−9.928	−37.394
	Female *short move*	0.263	7.419	−20.713
	Daylight duration *feed*	−1.294	−7.649	−13.556
	Daylight duration *move*	0.705	4.195	−1.75
	Daylight duration *short move*	0.342	4.572	−8.814
	Hunting period *feed*	−0.142	−4.788	−38.401
	Hunting period *move*	0.047	1.051	−21.048
	Temperature *feed*	0.008	1.832	−208.204
	Temperature *move*	−0.008	−3.783	−429.586
	Precipitation *move*	−0.052	−3.856	−77.558
Multipliers of the γ parameters (κ_{ik})	Female *feed (base = male)*	1.256	16.827	3.431
	Female *short move (base = male)*	0.908	17.357	−1.738
	Hunting period *move (base = outside hunting period)*	0.943	10.18	−0.608
Exponential term in γ multipliers (λ_{ik})	Daylight duration *feed*	1.804	5.071	2.261
	Daylight duration *move*	−0.695	−1.415	−3.451
	Precipitation *move*	0.013	2.414	−182.821
	Temperature *feed*	−0.045	−0.375	−8.624
Scale	Scale parameter (σ)	0.272	64.741	−173.423

Model performance: Final LL: −32116.1; AIC: 64282.21; BIC: 64443.52.

The climatic variables related to temperature and precipitation were obtained from the Swedish Meteorological and Hydrological Institute (SMHI). In particular, station-specific time series within the study area were converted using the R package “mba” (Finley and Banerjee, 2014) to interpolated raster series with a 5-day temporal resolution and a 5 km spatial resolution. To account for variation across the study area, the raster values of these climate variables associated with the area inhabited by each bear were averaged using a circular home range with a sex-specific average home range diameter (Bischof et al., 2018). In our models, we tested minimum, maximum and average temperature. Since the focus of our study is to understand how animals allocate time to different activities across 24 h, the mean temperature seemed to be the most appropriate measure. The R (R Core Team, 2020) library “maptools” (Bivand and Lewin-Koh, 2020) was used to determine the length of day, night, and twilight for every day during the berry season. We consider as “Daylight” the period between sunrise and sunset, “twilight” as the time period between sunset and nautical dusk (i.e., when the sun moves to 12° below the horizon in the evening) and from nautical dawn (when the sun moves to 12° below the horizon) to sunrise. The remaining time (i.e., between nautical dusk and dawn) is defined as “night”. Due to high correlation between *Daylight* and *Night duration* only the former variable has been retained in the model. This variable is also a good proxy for the time elapsed so far in the berry season, as the *Daylight duration* changes linearly in the study period. The dummy variable taking value 1 for the time between 21 August – 15 September is used to test whether the hunting season affects the bears’ behaviour. The MDCEV model was estimated using the “apollo” package (Hess and Palma, 2019) in R (R Core Team, 2020).

4. Model results

The final model results are presented in Table 3. We look first at the baseline parameters that relate primarily to the discrete choice, before looking at the satiation parameters that relate more to the continuous choice. The baseline parameters have limited interpretation (Bhat, 2018).

4.1. Shifts in the δ parameters

We found find that within a 24-h time span, older bears (aged 16 years or over) are more likely to *Feed* and less likely to *Move* compared to younger ones (cf. Table 3). The coefficient “Female short move” points to the fact that females are more likely to move than solitary males, suggesting that they are more likely to do a combination of activities in the given time frame. When the day lasts longer (i.e., at the beginning of the berry season), the baseline utility of moving and short moving increases, while that of foraging decreases.

The start of the hunting season has a significant effect on bear behaviour, i.e., the bears are more likely to move and less likely to feed (cf. Table 3). Interestingly, since in our application all activities are modelled jointly, we see that decreased probability of feeding is accompanied by increased probability of *moving*, with *short move* being unaffected.

We tested for the effect of daily temperature in different forms (i.e., min, max, range, average), and daily average temperature had the highest explanatory power and was retained in the final model specification. A higher likelihood of *Feed* and a lower likelihood of *Move* are associated with increases in temperature (Table 3).

The shift of the δ parameters as a consequence of precipitation (in mm) shows that an increase in this variable is linked with a lower likelihood to *Move*.

4.2. Multipliers of the γ parameters

The results related to the parameterisation of the γ parameters are shown in the bottom part of Table 3. Due to the fact that they enter the satiation equation multiplicatively, these parameters have a significant impact if they are significantly different from 1. Female bears are found to spend longer time in *Feed* and *Short move* as opposed to males. We also observe that during the hunting period, bears spend more time moving as opposed to outside of the hunting season. This indicates that not only the probability of *Move* increases due to hunting but also time spent in this activity increases.

The last set of parameters in Table 3 measure the sensitivity of the overall satiation to changes in continuous variables. Fig. 1 shows the impact of the duration of daylight on the satiation from *Feed* and *Move*, given the estimated values of λ_{ik}.

A positive value of this exponential term (cf. "Daylight duration *feed*") implies that as the duration of daylight increases, the activity (*Feed*) will be performed for longer. The opposite is true for *Move*. This implies that at the beginning of the berry season, if bears engage in *feeding,* they will do so for longer than at the end of the berry season. The opposite is true for *Move*. This is likely related to the fact that the end of the berry season corresponds with the hunting season, when bears feed less and move more.

The magnitude of the changes in satiation is determined by the value of the estimated parameters and the baseline value (γ_k*base*). Precipitation positively affects the value of the satiation parameter for *Move*, although its small value results in a slowly increasing trend (cf. Fig. 2). Higher temperatures imply a smaller amount of time spent foraging (cf. Fig. 3).

4.3. Model validation

In order to obtain a measure of how well our proposed model performs at capturing the trends in the data, we have carried out a prediction of the shares of days on which a given activity is carried out, as well as of the activity duration and compared it with the data. This is what is sometimes referred to as "base" prediction, i.e. applying the model without introducing any changes to the data. As shown in Table 4, the differences between the discrete and continuous choice statistics in the data and in the prediction are limited, and the RMSE is low in both cases, indicating that the model adequately replicates the behaviour in the data.

5. Discussion

In this paper, we present a proof-of-concept for the application of advanced econometrics models to understand the behaviour of wild animals. Addressing the limitations of previous studies, we produced a model of brown bear behaviour where we model engagement in multiple activities, considering not only which activities are conducted but also the amount of time invested in each. We showed how both the discrete and continuous outcomes are related to the characteristics of the animals themselves as well as to environmental variables and external factors (i.e. hunting). While the MDCEV modelling framework adopted was not previously used to improve the understanding of animal behaviour, we demonstrated how this tool can be suitable for our investigation by obtaining results in line with existing work as well as providing new insights made possible by the specific model structure.

To start with, our classifications of the different activities inferred via the GPS relocation data allowed us to unveil behavioural patterns correlated with bear characteristics. We showed that female bears are more likely to engage in the *Short Move* activity and do so for longer compared to males. This is an example of a finding allowed by the MDCEV model, i.e., capturing discrete and continuous behaviour contextually. As explained in the Methods section, this activity is most likely to be made up of a mixture of different

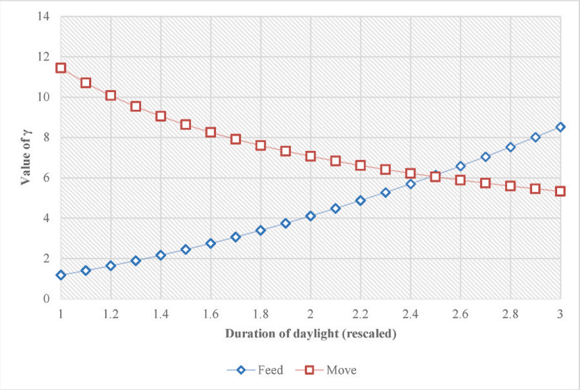

Fig. 1. Effect of the duration of daylight on satiation parameters.

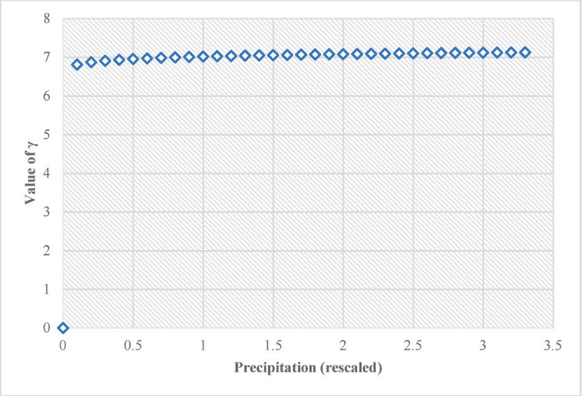

Fig. 2. Effect of the amount of precipitation on the satiation parameter for *move*.

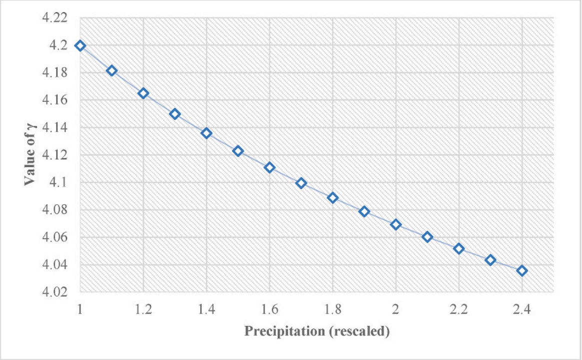

Fig. 3. Effect of temperature on the satiation parameter for *Feed*.

Table 4
Recorded and predicted values for the discrete and continuous choice.

Discrete choice (share of days with non-zero time in activity)			Continuous choice (hrs spent)	
Activity	Share in data	Predicted share	Average duration in data	Average predicted duration
Rest	1.00	1.00	8.73	8.56
Feed	0.99	0.99	6.00	5.95
Short Move	0.96	0.97	3.80	3.92
Move	0.96	0.95	5.47	5.58
RMSE = 0.12			RMSE = 0.01	

activities, implying that female bears have a more varied pattern of behaviour within each observed time slot. We have also shown that older bears are more likely to engage in foraging rather than travelling long distances.

Capturing both the discrete and the continuous outcomes allowed us to gain a more complete picture of behaviour, as we understand which characteristics are associated with activity duration instead of only providing insights on which activities are performed. A key result of our model is that during the hunting season, bears are less likely to feed and more likely to move – and do so for longer periods of time. This finding is in line with existing ecological literature which demonstrated that apex predators may perceive and respond to hunting risk similar to that of prey responding to a natural predator (Ordiz et al., 2011; Brook et al., 2012), forcing them to increase vigilance at the expense of foraging.

Our results conform well with Hertel et al. (2016b), who found that bears effectively responded to variation in risk during the day by decreasing their foraging activity in the morning hours of the hunting season and not changing their behaviour in the afternoon foraging bout, indicating that bears did not allocate antipredator behaviour to times of comparably lower risk. On the other hand, contrary to the existing literature, which has focused on modelling one activity (Hertel et al., 2016a; Hertel et al., 2016b, Mclellan, 2015; Steyaert et al., 2016), the MDCEV framework allows us to directly identify the trade-offs in bears behaviour. Bears reduce risk from hunting by increasing probability of Move and its duration, this happens at the cost of the forage activity. This shows that hunting affects the energy budget of bears in a more complex way than identified in the literature (Sahlen et al., 2015; Steyaert et al., 2016;

Hertel et al., 2016b), that is, not just by lowering energy intake by decreasing foraging activity, but also by increasing energy expenditure as they are more likely to Move and do it for a longer period. This shows that hunting season is highly costly for bears in terms of energy balance, as they are less likely to feed and more likely to move at this crucial time for their energy intake, i.e., before hibernation. The additive effect of reduced forage intake and higher engagement in movement is likely to result in poorer body condition upon den entry and may ultimately reduce winter hibernation survival and reproductive success. This result potentially enables managers and conservationists to better understand the ecology of this species as well as how people affect its behaviours and what are the consequences on energy expenditure and survival.

The sign and magnitude of the λ_{ik} parameters combined with the shift in the δ parameters (i.e. *Daylight duration Feed)* showed that as *Daylight duration* decreases, bears are more likely to *Feed* but will carry out this activity for a shorter period of time. Exactly the opposite pattern is true for *Move,* that is as *Daylight duration* decreases bears are less likely to *Move* but will carry out this activity for a longer period of time if it is conducted. The opposing trends displayed as time advances in the berry season indicates that bears constantly change (adapt) their foraging strategy during the studied period. A possible explanation of the observed phenomena is that at the beginning of the berry season, food is scarcer (or of lower quality) and once bears find a feeding place, they will carry out the *Feed* activity for longer, as there are no good alternatives available; whereas later in the berry season, when more berry species are available and food is more abundant, bears will travel between high quality spots. This interpretation is in line with what has been reported by Hertel et al. (2016b), who showed that in the berry season, bears are selective and navigate in the forest landscapes by using areas of higher than average berry abundance.

Overall, this study is innovative in two ways: it demonstrated the application of a state-of-the art discrete-continuous model to a new field of research, and it shows not only that results which are intuitive and in line with the literature can be obtained, but also that new insights can be added due to the more comprehensive approach looking at different activities and at both choice of activities and activity duration. In particular, this approach allowed us to distinguish cases of zero time in an activity (i.e. a corner solution) from small non-zero times, and that is allows for a study of satiation, i.e. non-linear gains in utility from additional consumption. In terms of specific conclusions for our case study, the proposed approached allowed us to observe that the disturbance due to hunting affects energy expenditure as it impacts on multiple activities, namely feeding and moving. It also allowed us to understand key differences across the animals. For example, we found that female bears not only engage in different types of activities (e.g. Short Move) but also do so for different durations with respect to their male counterpart.

Like any study, we acknowledge that our work has a number of limitations. The classification of the moving activity in two separate activities is subjective and while it helps with the interpretation of results, it might not be ecologically accurate, and could impact our findings. Especially in the case of *Feed* and *Move,* our activity classification is rather coarse with respect to studies using human data collected with smartphone or GPS trackers that can virtually capture any movement. This is a result of working at the level of 1-h data. Finer temporal resolution (i.e., GPS fixes every 30min or 15min) would allow for more reliable classification and understanding of behaviours, as it is likely that bears undertake a mixture of activities during 1h intervals. At the same time, this would be very battery-intensive and would require capturing and re-releasing bears more often to change the batteries, which is expensive and may not be possible due to animal welfare concerns. Additional improvement of the method could be achieved by linking the GPS data with other high-resolution data such as, 3D accelerometers, heart-rate sensors. Moreover, as this study aims to be a proof-of-concept, we only used a sub-set of the available data. Using a larger and more comprehensive dataset could unveil further patterns of behaviour, for example the ones of younger animals and females with dependent offspring. We leave these developments to future work, with the main aim of the present paper being to present the method and its potential.

Credit author statement

Chiara Calastri: Conceptualization, methodology, formal analysis, software, writing, Marek Giergiczny: Conceptualization, data curation, writing, Andreas Zedrosser: Data curation, reviewing and editing, Stephane Hess: Conceptualization, software, supervision, reviewing and editing.

Declaration of competing interest

The authors declare that there is no conflict of interest in relation to the contents of this work.

Data availability

The authors do not have permission to share data.

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