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Modelling movements of Saimaa ringed seals using an individual-based approach

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Abstract

Movement is a fundamental element of animal behaviour, and it is the primary way through which animals respond to environmental changes. Therefore, understanding the drivers of individual movement is essential for species conservation. The endangered Saimaa ringed seal (*Phoca hispida saimensis*) lives land-locked in Lake Saimaa and is affected by various anthropogenic factors. Telemetry studies provide critical information but are insufficient to identify the mechanisms responsible for particular movement patterns. To better understand these mechanisms and to predict how changed movement patterns could influence the subspecies' spatial ecology, we developed an individual-based movement model. We divided the seals' daily routines into foraging and resting and explored how well the model captured observed home ranges and other movement metrics. Here we present the model, its predictions of home ranges and its sensitivity to model assumptions and parameter uncertainty. We used movement data from one individual to calibrate the model, but this resulted in poor predictions of home range sizes of five seals used for validation. This suggests that differences in movement paths not only reflect different landscape configurations but also differences among the individuals' state and personalities. Therefore, we separately re-calibrated the model to data from five individuals, reproducing their home ranges, habitat use and movement paths more accurately. Although ignoring many aspects of seal behaviour, the model can be applied as a tool to guide further data collection and analysis, study seal ecology, and evaluate the efficacy of various conservation measures.

Key words: Bycatch mortality, Conservation, Home range, Pattern-oriented modelling, *Phoca hispida saimensis*, Saimaa ringed seal, Spatially explicit individual-based model

1. Introduction

Understanding the drivers of animal movement is essential for preserving populations and species. Movement, as with any other behaviour, is related to the resulting payoff of that particular action. Some types of movements, such as foraging, predator avoidance, or finding a mate, may produce proximate payoff; they are all important considering the ultimate goal of individuals: reproducing and passing genes forward (Nathan et al., 2008). Even though the ultimate driving forces behind movements are similar across species, there is a wide variety in movement patterns. Movement can be oriented towards or away from certain areas (Nathan et al., 2008), and the scale of the movements may vary from metres to thousands of kilometres depending on the species. Moreover, the individual variation within species is often remarkable (e.g. Austin et al., 2004; Ball et al., 2001; Schwarzkopf and Alford, 2002).

Animal movements can be studied using remote techniques such as telemetry (VHF or satellite tags). Use of tags enables observation of animal movements and habitat selection patterns. In addition to the location, tags can record environmental conditions or the physiological status of individuals. Telemetry techniques enable collecting large high-resolution datasets; therefore, the method has been widely applied in studying movements of species in many taxa from insects to large mammals (Chudzińska et al., 2016; Hake et al., 2001; Hart and Hyrenbach, 2009; Hedin and Ranius, 2002; Höjesjö et al., 2007; Rautio et al., 2013; Wabakken et al., 2007).

Telemetry data are typically analysed using a statistical approach that enables identification of home range sizes, activity patterns, variations in movement distances and auto-correlation in movement paths (e.g., Fleming et al., 2014; 2015). Such correlative studies help identifying relevant movement patterns such as distributions of step lengths and changes in directions, or of the time allocated to different movement-related behaviours (Morales et al., 2010; Van Moorter et al., 2009). Mechanistic models then can take these patterns into account (Pauli et al., 2013). Individual-based models (IBMs) are particularly suitable for this purpose, as they allow us to explicitly represent individual animals and their behavioural decisions. IBMs can be useful whenever variability among individuals, local interactions with other individuals or their abiotic environment, or adaptive behaviour are considered essential (DeAngelis and Grimm, 2014; Railsback and Grimm, 2012). Here, we combine telemetry data and individual-based modelling to develop a model capable of predicting Saimaa ringed seal (*Phoca hispida saimensis*) movement patterns and emergent home range behaviour. Next-generation ecological models are likely to be increasingly based on standardized sub-models that use first principles to represent mechanisms and behaviours such as foraging, movement and home range behaviour (Grimm and Berger, 2016). Therefore, our model could be used as a tool for seal conservation when integrated within a population model or coupled with other techniques.

Saimaa ringed seal is a subspecies of ringed seal that became isolated in Lake Saimaa, Finland, after the last ice age about 9,500 years ago (Nyman et al., 2014). The subspecies is categorized as endangered (Liukko et al., 2016), and currently, there are only about 350 seals (Kunnasranta et al., 2016). The population may have included up to 1,300 individuals at the end of the 19th century, but hunting and other direct and indirect anthropogenic factors brought the population almost to extinction (Kokko et al., 1999; Kokko et al., 1998; Sipilä, 2003). Conservation measures have been applied to tackle the problems, and the population size is slowly increasing. The main threats are currently bycatch in gillnet fishing, small population size, poor snow conditions for breeding, and human disturbances in the breeding period (Auttila, 2015; Liukkonen et al., 2017; Niemi, 2013; Valtonen, 2014). Conservation measures are widely based on scientific studies providing new information. In particular, several years of telemetry studies (Hyvärinen et al., 1995; Koskela et al., 2002; Kunnasranta et al., 2002; Niemi et al., 2013a; Niemi et al., 2012, 2013b) provide detailed information about Saimaa ringed seal behavioural ecology and movements.

Our model builds on the observation that seal movements consist of cycles of foraging in deep water areas (≥ 15 m) and resting on haul out sites next to small islands (Vincent et al., 2017).

Movements are based on both correlated random walks and unidirectional movements towards foraging areas and haul out sites. Correlated random walk has been widely used in movement modelling (Fagan and Calabrese, 2014), but it results in animals that gradually move away from their initial position (Nabe-Nielsen et al., 2013). To enable simulated seals to return to previously used haul out and foraging areas, we implemented a spatial memory component (Nabe-Nielsen et al., 2013). This addition of memory enables the formation of home ranges.

IBMs have been used to model movements of many species (Arrignon et al., 2007; Bennett and Tang, 2006; Linard et al., 2009; Nabe-Nielsen et al., 2013; Railsback et al., 1999; Reuter and Breckling, 1999) and have also been applied to conservation and management (Eisinger and Thulke, 2008; Eisinger et al., 2005; Liu et al., 2013; López-Alfaro et al., 2012; Nabe-Nielsen et al., 2010; Thulke and Eisinger, 2008). The ability to include highly detailed information about the environment and species make IBMs ideal for modelling endangered or economically important species (DeAngelis and Grimm, 2014).

The proximate purpose of our model is to simulate typical movement patterns of adult individuals to characterize the home range formation and spatial ecology of the species, but the model could ultimately be extended to study seal population dynamics under changing environmental conditions and different conservation measure scenarios. As with models for conservation biology in general, where we usually have too little data to develop models that deliver accurate predictions, our model is designed to be realistic enough for relative predictions, which allows us to rank different management options. Here, we present the model and compare its results with telemetry data. We started model development with the assumption that landscape complexity would explain the observed variation in home range sizes, and therefore parameterized the model for a single individual for which the richest data were available. After realizing that the resulting parameters did not explain the movement of other seals, we reverted to considering the distribution of the parameters of all observed individuals. We will discuss how this pragmatic and simplified approach relates to the unresolved problem of extracting movement parameters from tracking data of individuals with different personalities, moving in complex environments.

2. Materials and methods

2.1. Biological background

Here, we provide the background information that guided model design. Ringed seal ecology is relatively well known, but much of the knowledge does not apply to the Saimaa ringed seal, which lives in a freshwater environment that differs considerably from the oceanic environment inhabited by other subspecies. Adult Saimaa ringed seals have home ranges of around 90 km^2 on average (Niemi et al., 2012), which is remarkably smaller than home ranges reported in marine ringed seals (e.g., Born et al., 2004; Oksanen et al., 2015). For example home ranges of individual Baltic ringed seals may cover an area of over 12 000 km^2 (Oksanen et al., 2015), which is almost three times larger than the total surface area of Lake Saimaa. In addition to compact home ranges, seals' sedentary behaviour is apparent from strong haul out site and breeding site fidelity (Koivuniemi et al., 2016; Valtonen et al., 2012). Saimaa ringed seals reach sexual maturity at the age of 4–6 years (Auttila et al., 2016) and give birth in subnivean snow lair during period from mid-February to mid-March after 11-month gestation period (Sipilä, 2003). After the breeding, mother-pup pairs stay in close vicinity to the lair site until the pup is weaned at the age of approximately 3 months (Hyvärinen et al., 1995; Kunnasranta, 2001; Niemi et al., 2013a). Males and females that are not breeding also use snow lairs for moulting and resting in the winter time (Helle et al., 1984). When weather gets warmer in the spring, lairs collapse and seals start to haul out first on the ice, and later on terrestrial platforms. These are typically rocks located on the shoreline of small islands, but not in the vicinity of the mainland. According to telemetry studies, Saimaa ringed seal individuals use an average of 13 haul out sites during the open water season (Niemi et al., 2013a). Haul out takes over half of seals' time during the moulting period from late April to early June, with activity peaking in the afternoon when the temperature is highest, which is reported to be beneficial for moulting (Boily, 1995; Paterson et al., 2012). Outside of the moulting season, haul out takes no more than 20% of total time and is mainly nocturnal. Studies suggest that night time haul may be an adaptation to prey fish behaviour and disturbance, which is more frequent during the day (Hyvärinen et al., 1995; Kunnasranta, 2001; Kunnasranta et al., 2002; Niemi et al., 2013a).

Haul out is affected by many environmental factors (i.e., amount of solar radiation, wind, temperature and cloud cover), physiological status, and possible disturbance (Carlens et al., 2006; Moulton et al., 2005; Moulton et al., 2002; Niemi et al., 2013a). Especially in the case of the Saimaa ringed seal, disturbance by humans is an important factor affecting haul out, as the lake is a popular place for recreational activities (Niemi et al., 2013a). In addition to terrestrial sites, resting can also take place in water. Seals have been observed to make consecutive long duration dives that are suggested to be associated with resting (Hyvärinen et al., 1995; Kunnasranta et al., 2002). Sleeping dives usually take place next to haul out sites and are more likely to occur when the weather is not optimal for haul out, e.g., when it is raining. Still, even though resting is possible in water, haul out remains an important part of a seal's daily activities throughout the year, with a peak centred around the breeding and moulting seasons (Kunnasranta et al., 2002).

There is seasonal variation in Saimaa ringed seal feeding patterns. Seals' feeding activity is reduced during spring due to the breeding, nursing and moulting seasons. In late summer, seals need to forage actively to gain weight for the upcoming winter, as blubber is needed to provide protection from harsh thermal conditions. Seals are generalists that feed mainly on small schooling fish species, such as perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), vendace (*Coregonus albula*), smelt (*Osmerus eperlanus*) and ruff (*Gymnocephalus cernuus*) (Auttila et al., 2015; Kunnasranta et al., 1999) and use same water regions for feeding throughout the year (Auttila et al., 2015). Adult seals prefer deep water (≥ 15 m) foraging areas, where vendace and smelt, that are rich in fat content, are found outside spawning season (Kunnasranta et al., 1999). Other prey species are abundant in shallow areas throughout the year, and therefore seal foraging is not only limited to deep-water areas. The quantity of prey fishes is classified as medium to very high for perch and smelt in northern parts of the lake (Valkeajärvi et al., 2010) and food is not considered to be a limited resource (Auvinen et al., 2005).

Saimaa ringed seals have not been considered to be threatened by predators. However, recent findings have shown medium-sized carnivores (red fox *Vulpes vulpes* and raccoon dog *Nyctereutes procyonoides*) to be interested in ringed seal lairs (Auttila et al., 2014) and some pups are shown to be killed by a red fox (Auttila, 2015). Adult individuals are likely able to escape from predators more efficiently than pups, which are more prone to predation. Nevertheless, predation forms presumably only a minor part of Saimaa ringed seal mortality and it is focused only on pups during winters with poor breeding conditions (e.g. inadequate snow cover).

2.2. Study area

Lake Saimaa (surface area 4,400 km^2, mean depth 12 m) consists of several basins connected via narrow straits (Kuusisto, 1999). We focused on two water basins, namely Haukivesi and Joutenvesi (Fig. 1), together forming one of the most important breeding areas and it is inhabited by approximately 100 seals (Metsähallitus, 2016) comprising almost one-third of the estimated population.

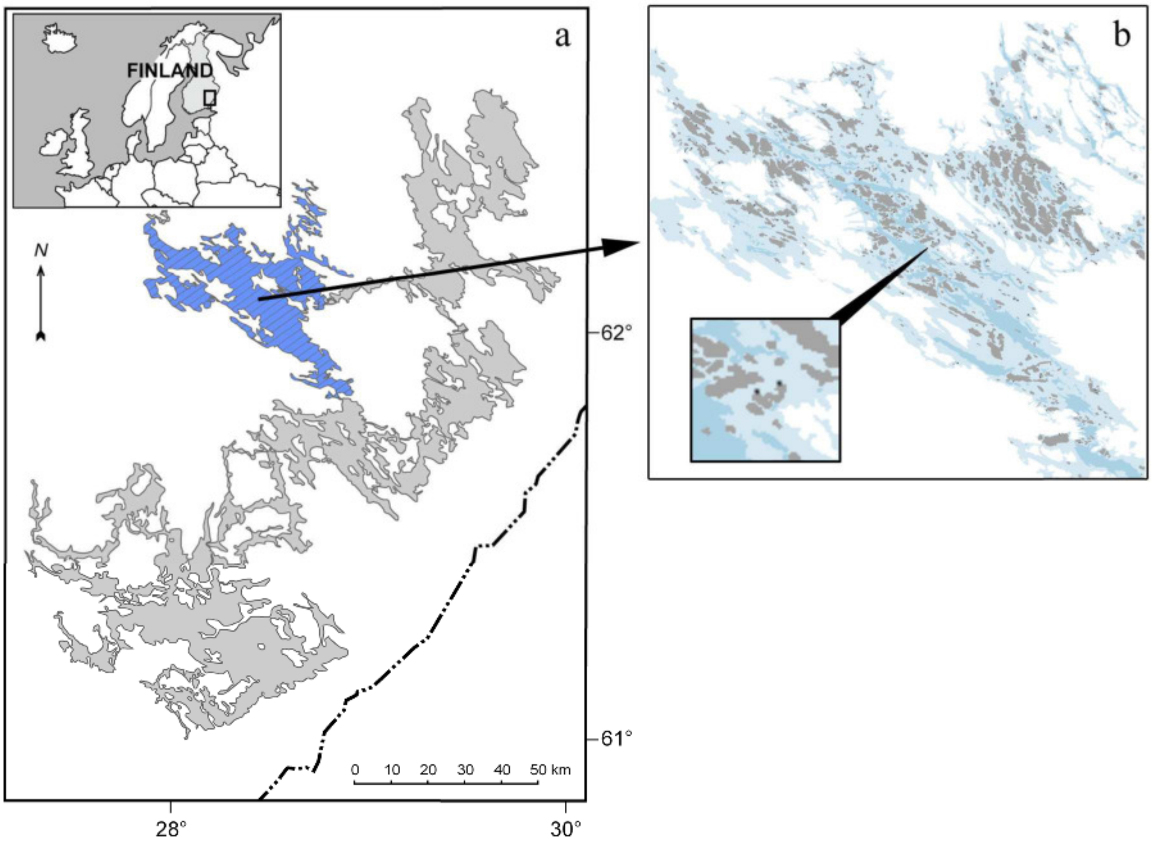

Fig. 1 Map of Lake Saimaa showing the Haukivesi and Joutenvesi basins (in blue) (a), which were implemented in NetLogo (b) (blue = water, dark blue = deep water (>15 m), white = land (>298 ha), grey = islands (1–298 ha), black dot = haul out site). Permit MML/VIR/TIPA/5012/17 © National Land Survey of Finland

2.3.Telemetry data

Data used in model development were obtained by equipping six seals with GPS/GSM tags (Sea Mammal Research Unit, St. Andrews University, UK). Seals were tagged in the Haukivesi basin between years 2007–2011 during the annual moulting season in spring. Neither of the two tagged females were pregnant or nursing offspring during the study season to our knowledge. Tags were set to record dive data (depth, duration), and to determine the location every 20 minutes if the seal was in the water and every 60 minutes if it was hauled out. A seal was considered to be hauled out if the wet/dry sensor on the tag had been dry for 10 minutes; the haul out was considered to have ended when the sensor had been wet for 40 seconds. In the first phase of pattern-oriented model development and parameterization, GPS-telemetry data from one adult male (ER11; 3822 relocations, tracking duration 125 days, mean swimming speed during the open water season; 424.10 m/20 min) from the study area were used to develop and calibrate the model. This individual had the highest resolution data in the database (Saimaa ringed seal telemetry database, University of Eastern Finland 2015). In the second phase, additional data from five adult individuals (HE07♀: 3003 relocations, 191 d, 367.15 m/20 min; KJ07♂: 4475 relocations, 218 d, 518.94 m/20 min; OL10♀: 2155, 180 d, 302.27 m/20 min; TO09♂: 3254 relocations, 194 d, 505.44 m/20 min; and VI09♂: 4618 relocations, 199 d, 281.88 m/20 min) were used for model validation and final calibration of one parameter (see section 2.5). All data were limited to the open water season and constrained to the same temporal resolution as the shortest tracking period, except for the initial calibration individual (ER11), whose data were fully used. AdehabitatLT package (Calenge, 2011) in R (R Development Core Team, 2011) was used for calibration. Additionally, datasets of 18 seals were used to develop probability distribution for the speed parameter (see section 4.3 Model sensitivity & Appendix E). These datasets were not used in model calibration.

2.4.The model

The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006; Grimm et al., 2010). Its implementation in NetLogo 5.2.0 (Wilensky, 1999) is available in the Supplementary Material. In addition, in the Supplementary Material (Appendix A), we provide a TRACE document ("TRAnsparent and Comprehensive model Evaludation") (Augusiak et al., 2014; Grimm et al., 2014; Schmolke et al., 2010) containing evidence that our model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

2.4.1 Purpose

The purpose of the model is to simulate seal movement patterns based on assumptions regarding resting and foraging behaviour.

2.4.2 Entities, state variables, and scales

The area represented in the model (Haukivesi and Joutenvesi basins) is 762 km^2. The model world consists of a grid of 1000 x 1000 cells, or patches; each patch represents an area of 0.00297 km^2 (54.5 m x 54.5 m). Model entities are habitat patches, seal and rock agents. Habitat patches are either land or water patches (land?; true/false). Some of the land patches were further characterized as island patches (island?; true/false). Land areas larger than 0.01 km^2 and less than 2.98 km^2 are considered islands in the model. The minimum size of an island preferred for haul out is reported to be 0.0002 km^2 (Niemi et al., 2013a) but was increased to 0.01 km^2 in the model to keep the habitat as realistic as possible while taking into account the limited resolution of the map. Water patches are divided into three categories: Deep water (≥ 15 m), shallow water (< 15 m) (deep; true/false), and water suitable for haul out sites (stone-place?; true/false). These are water patches next to islands where rocks are created, as such areas are regarded as suitable haul out sites. The number of potential haul out sites in nature is unknown and was thus estimated from haul out data and home range sizes. Observed average number of 13 haul out sites per seal per average home range size was extrapolated to the study area. Consequently, a total of 121 haul out sites were randomly created at initialization; this number is in accordance with an earlier telemetry study where it was observed that eight GPS/GSM tracked individuals used in total 104 different haul out sites in the same area (Niemi et al., 2013a). The sites used as starting points for seal agent were characterized only by their coordinates (init-site; x: 0–1000, y: 0–1000).

A seal is characterized by its age (age-in-months; 48 months), exhaustion level (exhaustion; 0.1–0.999), movement variables, including distance travelled in the time step (step-length; randomly set from a normal distribution, in metres) and direction of movement (turning-angle; 0–

360 degrees), and memory variables, including spatial memory of haul out sites and deep water areas (stone-cors; 0–100 sites, deep-cors; 0–100 sites), and the memory value of each visited haul out site (memory-stones-list; 0.1^{-7}–0.99); please note that due to memory decay model seals rarely remembered more than 5 sites. Only one seal is simulated at a time.

The time step is 20 minutes when the seal is swimming and 60 minutes when it is hauled out. This matches the resolution of data recorded with GPS/GSM tags. The ice-covered season (January–March) is omitted, as seal is moving in a smaller area within its home range (Kelly et al., 2010). The simulation starts at the beginning of April and is first run for 12.5 months; during the last 0.5 months of this period, the seal has its initial site as the only target for haul out. This warm-up period enables the seal to have some haul out sites and deep water areas in its memory before the actual data collection begins in the middle of consecutive April when the warm-up period of 12.5 months have passed. Results were then recorded after this warm-up period for duration of 4.17 months for individual ER11 and 5.96 months for the rest of the individuals.

2.4.3 Process overview and scheduling

The processes described below are executed in the same order in each time step (Fig. 2). Here, only summary descriptions of the processes are provided; see section 2.4.7 (Submodels) for details. Submodel names are given in italics:

(1) *Update time step* – Length of time step is updated, depending on the seal's activity.

(2) *Update age* – The seal's age (in months) is updated. Ice-covered season (January–March) is skipped by adding 3 months to the seal's age.

(3) *List coordinates* – Coordinates of the seal's location are added to a list for home range calculations.

(4) *Decay memory* – Memory values of the visited haul out sites are updated as memory decays over time.

(5) *Remember haul outs* – If the seal is currently hauled out, the site is added to memory.

(6) *Rest* – If the seal's exhaustion is above the moving threshold (see section 2.4.7 Submodels, Table 1) or there is a suitable haul out site near-by, it rests. The seal starts moving again when exhaustion decreases below the moving threshold. Movement mode is set to 1 (sets a deep water target patch) if there are deep water patches in the seal's memory and to mode 2 (correlated random walk) if that is not the case.

(7) *Move* – There are three different movement modes: movement to a previously visited deep water patch (mode 1), correlated random walk (mode 2), and movement towards a haul out site (mode 3).

(8) *Write results/Update plots* – Output files are written, and plots are updated.

Fig. 2 A simple flow diagram of processes in the Saimaa ringed seal movement model. Processes in the middle box are performed with each time step; depending on the movement mode, different additional procedures are executed. Boxes with dashed lines indicate the state criteria when the movement mode is switched.

2.4.4 Design concepts

The design concepts *Interaction* and *Collectives* do not apply to this model. *Adaptation*, *Objectives*, and *Prediction* are represented implicitly in the imposed haul out behaviour.

Basic principles – Seal movements consist of cycles of foraging in deep water areas and resting on haul out sites. The seal remembers visited haul out sites and foraging areas to some extent, which has influence on the space use. In addition, we implicitly represent bioenergetics as exhaustion, which requires haul out and increases with foraging time.

Emergence – Movement patterns, as characterized by the size of animal home ranges and time spent either moving or hauled out, emerge partly from animal personalities. Hence, in the model, different personalities appear as different speed parameter values for individual seals. Furthermore, the capacity and permanence of the seal's memory of visited haul out sites and foraging areas plays a role in the emergence of movement patterns. In addition, the location and number of potential haul out sites in the area affect the seal's movements in the model.

Learning – The seal learns about its habitat by remembering visited haul out sites and deep water grid cells.

Sensing – The seal senses and avoids land in its moving direction. It also senses if it is in a deep water area or if there is a haul out site nearby, and it knows the distance to visited haul out rocks.

Stochasticity – Step length in all movement modes and moving direction in movement mode 2 (correlated random walk) are drawn from truncated normal distributions. In addition, the positions of haul out sites are randomly assigned at initialization. Furthermore, haul out sites and deep water foraging areas that seal uses may differ among replicates; this introduces another factor creating stochasticity.

Observation – Position, distance from home (km), movement duration (h), and duration of haul outs (h) are measured every time step. Home refers to the location where the seal is initialized.

2.4.5 Initialization

The world is created by importing GIS shape files for water, deep water (≥15 m) and land areas. A total of 121 haul out rocks (see section *2.4.2 Entities, state variables, and scales* for estimation of number of haul out sites implemented) are randomly created near islands. One seal is created and positioned on a user-defined haul out site, set to resting mode, and given an empty memory except for the current haul out site, an exhaustion of 0.998 (maximum exhaustion 0.999) and an age of three months.

2.4.6 Input data

The model does not include input of data representing time-varying environmental drivers.

2.4.7 Submodels

Model parameters are listed in Table 1.

Table 1 Model parameters and their meanings, values and units. In addition, the procedures where the parameters are used are listed. All parameter values were obtained through calibration.

Parameter name	**Meaning**	**Value**	**Units**	**Procedure where used**
exhaustion-threshold	Determines when to head to a haul out site	0.500	–	*Move*
moving-threshold	Determines when to start moving after resting	0.100	–	*Rest* *Sleep-in-water*
exhaustion-recovery-rate	The rate at which exhaustion decreases when resting	0.660	per 60 min	*Rest* *Sleep-in-water*
ref-mem-decay-rate	Memory decay rate	0.210	per 60 min	*Decay-memory*
exhaustion-rate-adults	Exhaustion rate	0.089	per 20 min	*Set-exhaustion-rates*
mean-speed-adults	Mean speed value	100.000–350.000 depending on the individual used in parameterization	m/20 min	*Adjust-speed*
sd-speed-adults	Standard deviation of speed	123.100	m/20 min	*Adjust-speed*
mean-turning	Mean turning angle	0.109	degrees	*Adjust-turning-angle*
sd-turning	Standard deviation of turning angle	15.680	degrees	*Adjust-turning-angle*
land-distance	The distance how far seal can see when avoiding land	3.458	grid cells	*Avoid-land-decision*
ho-distance	Maximum distance to haul out site, which initializes resting if seal is not exhausted	6.000	grid cells	*Move*
ho-exhaustion-limit	Exhaustion must exceed the parameter value to initialize resting if seal is not exhausted	0.150	–	*Move*

2.4.7.1 Update time step, age and time

The time step is set to 20 minutes if the seal is moving and to 60 minutes if it is hauled out. Age and current time are updated accordingly.

2.4.7.2 List coordinates

Coordinates of the seal's location are stored in a list for home range estimations. Because the time step is three times longer (60 min) when hauled out, every pair of haul out site coordinates are listed three times to avoid bias in the results by emphasizing relocations when moving. In addition, only 25% of movement coordinates are listed to match the resolution of telemetry data. GPS/GSM tags fail to connect to the satellites occasionally, and therefore, the locations may not be obtained every 20 minutes as programmed.

2.4.7.3 Decay memory

The seal remembers visited haul out sites. However, memory decays over time (i.e., seal forgets). The last haul out site on the list will be removed if there are already 100 sites in the memory or if the memory value for a site is < 10^{-8}. Memory decay is represented according to Nabe-Nielsen et al. (2013):

$$M[c]_{t+1} = M[c]_t - (M_R \times M[c]_t \times (1 - M[c]_t)) ,$$

where t is time in units of time steps, $M[c]$ is the memory of a location c (unitless), and M_R is the reference memory decay rate (1/h).

2.4.7.4 Remembering haul outs

If the seal is hauled out, the site is added to its memory and given a memory value of 0.99. In cases where the site is already in the seal's memory, the entry representing the earlier visit is removed.

2.4.7.5 Rest

If the seal is hauled out or sleeping in water, exhaustion decreases following:

$$E[c]_{t+1} = E[c]_t - (R_R \times E[c]_t \times (1 - \frac{E[c]_t}{E[c]_{max}})) ,$$

where t is time, $E[c]$ is the exhaustion level, $E[c]_{max}$ is the maximum of exhaustion level, and R_R is the exhaustion recovery rate. If exhaustion falls below the moving threshold, the exhaustion level is set to 0.1 and either movement mode 1 or 2 is selected (see below for definition of movement modes).

2.4.7.6 Move

2.4.7.6.1 Movement modes

There are three movement modes that the seal can perform. After hauling out (during which movement mode is *false*), the seal heads to a deep water patch to forage (mode 1); having reached the target deep water grid cell, it starts moving by correlated random walk (mode 2). After foraging, the seal selects haul out site based on distance and memory factors and goes there to rest (mode 3). The choice between these three movement modes is based on the state variable *exhaustion*. When the seal is hauled out, its level of exhaustion decreases; once it decreases below the *moving threshold*, either movement mode 1 or 2 is selected. The seal heads to an earlier visited deep water patch (mode 1) if it knows any, or starts moving by correlated random walk (mode 2) if it has not visited any deep water areas yet (e.g., at the initialization of the model). Once a deep water area is reached, movement mode 2 is set (provided that the seal was not in mode 2 already). When *exhaustion* reaches the level of parameter *exhaustion threshold*, movement mode 3 is selected and the seal goes to a haul out site to rest and the movement mode is set to *false*. Alternatively, the seal can also rest when there is a suitable haul out site within distance of the parameter *ho-distance*. This heuristic assumption of allowing the seal to haul out on near-by haul out sites, even if not fully exhausted, seems appropriate as it allows the seal to save energy. If *exhaustion* exceeds its maximum value before reaching a haul out site, the seal sleeps in water until exhaustion decreases low enough and it starts moving again. The *sleep in water* procedure is not possible in deep water.

The following processes are common to all movement modes and are performed before moving in the order listed:

(1) *Adjust step length* — Step length is drawn from a normal distribution with its mean set to the parameter *mean-speed-adults* and its standard deviation to *sd-speed-adults*. Minimum step length is set to 0.1 to avoid seals moving backwards.

(2) *Adjust turning angle* — Turning angle is drawn from a normal distribution with its mean set to the parameter *mean-turning* and its standard deviation to *sd-turning*.

(3) *Set exhaustion rate* — Exhaustion rate is set to the value of parameter *exhaustion-rate-adults.*

(4) *Update exhaustion level* — Exhaustion level increases in every movement step according to:

$$E[c]_{t+1} = E[c]_t + \left(Exh_R \times E[c]_t \times \left(1 - \frac{E[c]_t}{E[c]_{max}}\right)\right),$$

where Exh_R is the exhaustion rate, and *E*[c] is the exhaustion level (unitless).

(5) *Remember deep* — If the seal is in a deep water patch, the patch is added to the seal's memory. Earlier visits to that patch are removed from memory. If a target deep water patch is within the step length or a shorter distance, the seal moves there.

2.4.7.6.2 Targeted vs. non-targeted movements

Earlier described movement modes can be further divided into targeted and non-targeted moving. In *non-targeted moving*, the seal moves by correlated random walk (mode 2). The turning angle is updated every time step, land is avoided if necessary, and a step is taken forward. In *targeted moving*, movement is directed either towards a deep water foraging area (mode 1) or a haul out site (mode 3). If the seal is moving towards a deep water area, one deep water grid cell is randomly selected from the seal's memory and set as a target. The selection of the target haul out site is based on the distance from the seal's position and time when the seal last visited that site, as described below.

Calculate haul out site attraction value — Target haul out site is chosen by calculating the attraction values of previously visited haul out sites as follows:

$$A\ [c]_t = \frac{1}{M\ [c]_t} \times D\ [c]_t$$

where A [c] is the attraction value of the site, M [c] is the memory value of the site (see submodel *decay-memory*), and D [c] is the distance of visited haul out sites to the seal. The haul out site with the smallest value is chosen as a target.

2.4.7.6.3 Avoid land

The design of the land avoidance procedure used the approach described by Dalleau (2013). A flow diagram of the procedure is presented in Figure 3. This submodel consists of four different procedures:

(1) *See if there is land ahead* — The seal checks if there is land ahead within one step length or less. Distances smaller than one step length are needed to avoid the seal jumping over narrow land areas.

(2) *Avoid land decision* — Land avoidance direction selection, i.e., left or right, is based on two steps. First, the seal turns 45 degrees left and right and calculates which turning direction has less land within an angle of 90 degrees and a radius defined by the parameter *land-distance*. If there is an equal amount of land in both directions, the moving direction is chosen randomly.

(3) *Avoid land right* — First, the seal checks if there is land ahead in its moving direction (*see if land ahead*). If not, the seal turns counter-clockwise in steps of 10 degrees until it detects land in its moving direction. Then, the seal chooses the previous turning direction and takes a step forward. This makes the seal follow the shoreline of an island. If the *Avoid land decision* was set to right at the beginning of this procedure, the seal will avoid it from the right side of the detected land. It turns clockwise in steps of 10 degrees until there is no land ahead and then takes a step forward. If the seal has already turned 360 degrees and has not encountered land, it takes a step towards the set target. Sometimes the step length is long enough to make the seal encounter land in every direction. In such case, step length is reduced by 50% and the land avoidance procedure is repeated; this reduction is repeated until the seal can move. When the angle between seal's current heading and its target is small ($\leq 45°$), land is most likely avoided. If there is no land ahead, and the angle between heading and target is ≤ 45 degrees, land avoidance mode is turned off.

(4) *Avoid land left* — This procedure is identical to *avoid land right*, except that the seal turns clockwise if there is no land in its moving direction and counter-clockwise if there is. This makes the seal avoid land from the left side.

Fig. 3 Flow diagram of land avoidance decision-making in the Saimaa ringed seal movement model.

2.4.7.7 Write results/Update plots

The output variables *distance from home* and *moving duration*, and additionally coordinates of seal movements for home range estimations are written into an output file. Plots of the seal's distance from home, moving duration and haul out duration are updated every time step.

2.5.Parameterization

The model was developed, parameterized and tested following the pattern-oriented framework (Grimm and Railsback, 2012; Grimm et al., 2005) in two distinct phases. Nine parameters were inversely determined (Grimm and Railsback, 2012; Wiegand et al., 2003) via calibration of two movement patterns obtained from one tracked male (ER11; see section 2.3). The patterns used were *moving duration* and *distance from home* and these were measured from both simulated and telemetry tagged seals. Home represents the location where the seal was captured for telemetry data, but in the model it refers to the initial position of the seal. *Distance from home* was recorded at each time step, and *moving duration* was measured when the seal reached haul out site after a foraging bout. Parameter estimation was performed in two rounds: first, parameters were varied over a large range (exhaustion-rate-adults; 0–1.00, mean-speed-adults; 0–600.00, sd-speed-adults; 0–200.00, mean-turning; -10.00–10.00, sd-turning; 0–180.00, ref-mem-decay-rate; 0–1.00, land-distance; 1.00–10.00); second, they were fine-tuned by being varied over a narrower range around the optimal values identified in the first round (exhaustion-rate-adults; 0.05–0.09, mean-speed-adults; 100.00–300.00, sd-speed-adults; 100.00–200.00, mean-turning; -5.00–5.00, sd-turning; 10.00–60.00, ref-mem-decay-rate; 0–0.35, land-distance; 3.00–10.00). In both cases, a Latin hypercube sampling design (Iványi et al., 1979) was used by means of the *tgp* R package (Gramacy, 2007; Gramacy and Taddy, 2010) to draw 800 parameter sets from the entire parameter space defined by the nine parameters selected for calibration. For each parameter set, the model was run ten times; means of the output variables' medians were calculated and compared to telemetry data to assess model performance. Deviation from telemetry data was calculated according to:

$$Deviation = \frac{|Obs - Sim|}{Obs},$$

where *Obs* is the observed median for the two variables calculated from the telemetry data, while *Sim* is the mean of the model runs' medians of the given output variables.

Based on the first round of simulations and following a filtering approach (Wiegand et al., 2004), the parameter sets having a deviation for the *moving duration* variable below 15% were selected; among the sets passing this first filter, only the parameter sets presenting a total combined deviation for both patterns below 500% were retained to determine the range for the second round of simulations. In this stage, the parameter set producing the lowest total deviation from telemetry data was chosen.

Since the duration of haul out events is influenced only by exhaustion recovery rate, we calibrated this parameter alone via a sensitivity experiment (parameter range 0-1.00, steps 0.01). Exhaustion recovery rate was calibrated to allow seals to haul out for the time observed by Niemi et al. (2013a). Haul out does not include any stochastic elements among runs; therefore, one run per parameter value was performed. The variation within runs arises from the state of an individual entering haul out (i.e., exhaustion level). The parameter value producing the lowest deviation in comparison to telemetry data was chosen.

In order to enable seal haul out not only when it is exhausted but also when there is a suitable haul out site nearby, parameters *ho-distance* and *exhaustion-ho-limit* were added (see Table 1 for parameter description) and calibrated (*ho-distance;* values tested 0.1, 2.0, 4.0, 6.0, 8.0, 10.0; *exhaustion-ho-limit;* values tested 0.10, 0.15, 0.20, 0.25; 0.30). *Ho-distances* determines the distance from which a seal can observe a haul out site and *exhaustion-ho-limit* sets the minimum value of exhaustion at which haul-out can be initialised to avoid a seal starting to haul out right after a previous haul out event. Parameters were calibrated to match the observed pattern of calibration individual and the parameter values resulting in the highest number of replicates that did not statistically differ from the observed datasets (one-way ANOVA, $p > 0.05$) were selected.

The model was not able to reproduce the *distance from home* pattern of the five individuals used for validation (see results section 3.2). Since the global sensitivity analysis (see results section 3.3) indicated that the *mean-speed-adults* parameter had the strongest effect on this model output, we calibrated this parameter separately for the five individuals used for model validation (tested ranges: ER11; 60–210 m/20 min, HE07; 250–400 m/20 min, KJ07; 250–400 m/20 min, OL10; 10–160 m/20 min, TO09; 110–300 m/20 min, VI09; 20–250 m/20 min). Simulations were replicated ten times. The parameter values resulting in the highest number of replicates that did not statistically differ from the observed datasets (one-way ANOVA, $p > 0.05$) were selected.

2.6. Sensitivity analyses

We conducted a global sensitivity analysis to identify the model parameters with the strongest influence on model outputs. We applied the variance-decomposition technique of Sobol (1993) to decompose the model outputs' variance into variances attributable to each input parameter while also evaluating the interaction between parameters. Sobol first-order sensitivity indices (S_i) measure the effect of varying a focus parameter alone but averaged over variations in other input parameters, thus providing information on the average reduction of output variance when the parameter is fixed. The total-effect indices (S_{Ti}) measure the contribution to the output variance of the focus parameter, including all variance caused by its interactions, of any order, with any other input parameters. We used the *sensitivity* R package (Pujol et al., 2016), which implements the Monte Carlo estimation of the Sobol's indices using the improved formulas of Jansen (1999) and Saltelli et al. (2010). The number of tested settings was given by $m \times (p + 2)$, where m is the size of the Monte Carlo sample matrix and p is the number of parameters to analyse.

We selected seven parameters that varied over the following ranges: Exh_{adult} (exhaustion-rate-adults; 0.01-0.25), sl_{adult} (mean-speed-adults; 10-600), $sl\mathrm{SD}_{\mathrm{adult}}$ (sd-speed-adults; 10-600), ta_{adult} (mean-turning; -10 - +10), $ta\mathrm{SD}_{\mathrm{adult}}$ (sd-turning; 10-100), M_{R} (ref-mem-decay-rate; 0-1), and *Vis* (land-distance; 1-10). We chose a sample matrix of size 400, and Sobol first-order and total-effect indices were computed for each parameter from a total number of runs of $400 \times (7 + 2) = 3600$.

The sensitivity analysis examined two model outputs: *moving duration* and *distance from home*. Because the locations of haul out sites most likely influence the patterns, we simulated each of the parameter combinations keeping the same haul out site positions through all runs. The simulations were performed for 4.066 months as long as the movements of the calibration individual were monitored in 2011. Model runs were replicated 2 times.

To study the effects of the number and location of haul out sites, we ran simulations initialising the model with 120, 240, 480, 960 and 1920 rocks. Haul out sites were either kept in the same locations between replicates or randomly distributed at the beginning of each replicate. In both scenarios, simulations were replicated five times at each haul out site density. Simulations were initialised from the location where the individual used in model parameterization (ER11) was captured in the field survey, and the model was run for 4.17 months. Furthermore, we examined the extent to which the initial selection of haul out sites and deep water areas during the warm-up period influenced model outputs. To do this, the seal was initialised having five fixed haul out sites and deep water patches in its memory; the obtained results were compared to simulations run using the normal settings, i.e., empty memory. Simulations were replicated 15 times, and the model was run for 4.17 months in each replicate.

3. Results

3.1. Calibration

Results of the 10 replicates with the optimal parameter set (Table 1) indicated that the model reproduced the range of values of the two tested patterns reasonably well. Regarding the *distance from home* variable, 2 out of 10 replicates did not statistically differ from the field data (mean of the model replicates' means; 2.15 km, range 0.90–5.20 km), and in the case of *moving duration* pattern, 5 out of 10 replicates did not differ from the calibration dataset (mean of the model replicates' means; 11.68 h, range 9.11–15.33 h) (Fig. 4, see also Appendix B).

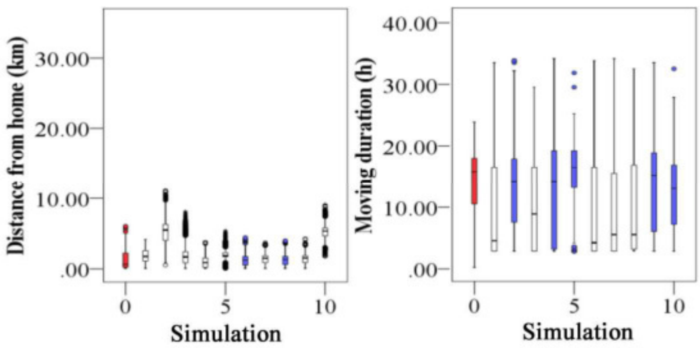

Fig. 4 Distance from home (km) and moving duration (h) data of the Saimaa ringed seal individual (ER11) used for calibration compared to 10 simulation replicates (0 = observed data from seal individual (red colour), 1–10 = simulation replicates). Simulations with no statistical differences from observed data (one-way ANOVA, $p > 0.05$) are marked with blue. (○ = outliers 1.5 × inter quartile range (IQR) or more above the third quartile or 1.5 × IQR or more below the first quartile, ⋆ = outliers 3 × IQR or more above the third quartile or 3 × IQR below the first quartile.)

3.2. Validation

After calibration, we tested the model performance on five independent datasets. There were large differences between the recorded datasets, and the model was not able to reproduce all the patterns observed in nature (Fig. 5, see also Appendix B). Furthermore, large variation among replicated simulations decreased model fits. The simulated distance moved from home and time between consecutive hauls were generally close to the average values observed in nature, and although there was a large variation in movement patterns among the satellite tracked animals, the range of values produced by the model were within the range of values observed for most satellite tracked animals. Still in the case of the *distance from home* pattern, there were statistically significant differences (one-way ANOVA, $p < 0.05$) in all replicates compared to field datasets. The *moving duration* pattern was well reproduced for individuals HE07 and KJ07 (the number of replicates that did not statistically differ were 9 and 8 out of 10, respectively).

Fig. 5 Distance from home and moving duration of five GPS/GSM tracked Saimaa ringed seal individuals compared to 10 simulation replicates (0=observed data from five seal individuals (red colour), 1–10=simulation replicates). For both output variables, box plots on the left are based on calibration on one individual (ER11); boxplots on the right where obtained after recalibrating the mean speed parameter on an individual basis. Simulations with no statistical differences from observed data (one-way ANOVA, $p > 0.05$) are marked with blue. (○ = outliers 1.5 × inter quartile range (IQR) or more above the third quartile or 1.5 × IQR or more below the first quartile, ⋆ = outliers 3 × IQR or more above the third quartile or 3 × IQR below the first quartile.)

3.3. Sensitivity analysis

The global sensitivity analysis showed that variations in *moving duration* were driven only by the exhaustion rate of adults, while the mean swimming speed of adults had the strongest effects on the variable *distance from home*. Interactions between parameters were more important in the latter variable (Fig. 6).

Fig. 6 Sensitivity analysis showing how (a) moving duration and (b) distance from home are influenced by changes in parameter values. ●= first-order indices ▲= total-effect indices

The number of haul out sites had a significant effect on both output variables (full factorial two-way ANOVA, *distance from* home; $p < 0.001$, *moving duration*; $p < 0.001$). The distribution of haul out sites (random distribution at the initialisation of each replicate or same locations in all replicates) had a significant effect on *distance from home* pattern ($p < 0.001$). There was no effect on *moving duration* ($p = 0.104$). Furthermore, the interaction between the number and distribution of haul out sites had significant effects on both patterns (*distance from* home; $p < 0.001$, *moving duration*; $p < 0.001$) (see also Appendix C). In addition, the stochastic selection of haul out sites and deep water foraging areas during the warm-up period increased variability between replicates. The standard deviation of the mean was higher for both output variables when selection of haul out sites and deep water foraging areas were based on memory and distance factors (*distance from home*; 0.32 km, *moving duration*; 1.29 h) compared to simulations in which sites were predetermined (*distance from home*; 0.16 km, *moving duration*; 1.01 h). The coefficient of variation of *distance from home* and *moving duration was* 65.75% and 29.97%, respectively, when the sites were selected based on memory and distance factors, and 64.84% and 32.77%, respectively, when sites were predetermined (see also Appendix D).

3.4 Re-calibration and evaluation of model performance

A high degree of variation among satellite tracked animals resulted in deviations from the simulated tracks. We introduced individual variation and re-calibrated the *mean swimming speed* parameter for each dataset separately to improve the model fit on observed *distance from home* patterns, as we observed that the swimming speed parameter had the strongest effect on this pattern in the global sensitivity analysis. Re-calibrated mean speed values were: HE07-250 m/20min, KJ07-350 m/20min, OL10-100 m/20min, TO09-190 m/20min and VI09-100 m/20min. After re-calibrating this parameter, the fit for both output variables improved. Regarding the *distance from home* variable, all five tested individuals had a reasonably good fit. In the case of *moving duration* variable, the model reproduced patterns relatively well for three out of five tested datasets (Fig. 5, see also Appendix B). For visualization purposes, we plotted the movement paths of individuals ER11 and VI09 compared to their corresponding simulations (Fig. 7).

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Fig. 7 Movement paths of Saimaa ringed seal individuals ER11 (a) and VI09 (b) on the left, and their corresponding simulations (one replicate) after re-calibration (see section 2.5 Parameterization) on the right. Box plots for the output variables, distance from home (km) and moving duration (h), are presented on the right (0 = observed data from seal individual, 1 = simulation replicate). (○ = outliers 1.5 × inter quartile range (IQR) or more above the third quartile or 1.5 × IQR or more below the first quartile.)

4. Discussion

We analysed existing telemetry datasets of six Saimaa ringed seals and used them to develop an individual-based movement model for adult seals. We based the model on assumptions regarding seal resting and foraging behaviour and their ability to memorise these sites. Our aim was to design and implement a seal movement model that could be further developed into a population model and used for evaluating efficiency of conservation measures. We analysed the model to test whether it could reproduce observed patterns of independent datasets that had not been used in model calibration. Furthermore, we tested its sensitivity to model assumptions and parameter uncertainty.

4.1. Model structure, innovations and limitations

The model is based on correlated random walk, a classical approach for modelling animal movements. However, correlated random walks cause animals to gradually move away from their starting position; therefore it is not optimal for modelling compact home ranges. To enable the formation of home ranges similar to those observed in Saimaa ringed seal telemetry studies, we added spatial memory in the model. Nabe-Nielsen et al. (2013) applied the concept of spatial memory (Van Moorter et al., 2009) on the model of harbour porpoises (*Phocoena phocoena*) to allow them memorise high quality feeding grounds and previously visited areas. We used the approach to have seal memorise foraging areas and haul out sites it used. The seal remembers not only the locations of visited haul out sites, but also the time since the last visit. The seal prefers haul out sites that are nearby and recently visited, leading to the emergence of home ranges (Vincent et al., 2017). Nabe-Nielsen et al. (2013) applied their model in a fairly homogenous landscape, which is in accordance with many of the existing movement models. In contrast to earlier memory-based movement models, we represented the environment in more detail. Spatial explicitness is especially important in models intended for management purposes (DeAngelis and Yurek, 2017). Lake Saimaa is a highly complex and labyrinthine environment (> 13 000 islands) (Kuusisto, 1999) and at the same time, a large variation in home range sizes have been previously reported for the Saimaa ringed seal (Niemi et al., 2012). Therefore, we hypothesized that the complex nature of the landscape may explain some of the individual differences in home rage size and shape. We developed and implemented a novel land avoidance procedure that is a key feature of our model (Dalleau, 2013). Land avoidance enables seal to bypass any land area it encounters while foraging.

Bioenergetics is an important feature of animal movement models and has been incorporated in detail in many IBMs (e.g. Bennett and Tang, 2006; Hölker and Breckling, 2005; Morales et al., 2005; Reuter and Breckling, 1999). We use exhaustion to model seal bioenergetics. The parameters were calibrated to match the movement patterns of one individual, as no ringed seal bioenergetics data is available. Implementing seal bioenergetics in more detail would likely result in more realistic presentation of the real system. First step for this could be addition of the existing dive data as diving behaviour unarguably has effect on the overall distance seal travels. In the current model version, we model only two-dimensional space use.

Some adult Saimaa ringed seal individuals stay within relatively small range while others take trips of tens of kilometres (Niemi et al., 2012). Because of this variation, capturing all these factors in a single value of parameters is a challenging task. Sex, age, body mass or other physical attributes were not considered in either model development or validation as it is not clear how these factors affect movement parameters of adult Saimaa ringed seals. Furthermore, it is not known to what extent the individuals' knowledge and experience of the environment affects their movement patterns. Older and more experienced individuals are likely to have more knowledge about the environment since Saimaa ringed seal are known to exhibit high site fidelity, which can affect their spatial behaviour. All data used in this study were obtained from individuals that were classified as adults based on their size. Even though sex-related variation have not been clearly reported in telemetry studies, genetic data show a sevenfold male-to-female gene flow ratio, indicating a larger scale of movement in males in the long term (Valtonen et al., 2014). Furthermore, sex- and body mass-related variations in movements are observed in grey seals (*Halichoerus grypus*) and ringed seals (Austin et al., 2004; Beck et al., 2003) , but no clear patterns are reported for Saimaa ringed seals. In general, body mass correlates positively with the extent of movements in mammals (Harestad and Bunnel, 1979; Lindstedt et al., 1986; Swihart et al., 1988). Nevertheless, Saimaa ringed seal movement patterns vary among individuals depending on their state, but such variations are not included in this model. Adding such variations might help explaining the difference in the movement patterns between satellite tracked and simulated seals.

In addition to biological factors, uncertainty and lack of environmental variables in the model may have impaired the performance. Location and number of haul out sites in Lake Saimaa may vary from one year to another due to water level fluctuations. Therefore, our estimates on haul out site number and location are not necessarily accurate which might have affected the model performance. Nevertheless, the number of haul out sites implemented in the model is in accordance with Niemi et al. (2013a) who observed eight GPS/GSM tagged seal to occupy 104 haul out sites in total in same study region. In addition to the uncertainty related to haul out sites, it is likely that e.g., disturbance, quality of surrounding environment in terms of foraging areas, lair sites, and mating partners, affect the space use of the seals in the real environment. In order to improve the model fit, data on environmental factors possibly affecting seal movement patterns should be collected and implemented in the model (Schick et al., 2008) as such data is non-existent currently. Likewise, the selection and change of haul-out sites can be affected by anthropogenic disturbances (e.g., boat passing by); data on the frequency of such disturbances could increase the fit of our model to movement data.

4.2. Model parameterization and validation

We used pattern-oriented calibration to find the best parameterization of the model. However, simulations run with the optimal parameter set yielded a poor fit to the independent telemetry datasets used for validation; the model was not able to reproduce the *distance from home* patterns recorded in the field, which were highly variable between tracked seals.

The Saimaa ringed seal shows large intraspecific variability in movement patterns and spatial ecology (Niemi et al., 2012); particularly, our field datasets revealed strong variations across individuals in their swimming performance, which has a strong effect on the movement distances simulated by our model. To implement the intraspecific variability in swimming performance observed in nature in our model, we re-calibrated the mean swimming speed parameter on an individual basis using data from the five individuals that we initially used for validation, which led to a significant improvement in model performance. Furthermore, we observed large variability in exhaustion rates between seals; therefore, calibration of the *exhaustion-rate* parameter on an individual basis would likely result in a better fit for the moving duration pattern, as this parameter was observed to have the strongest effect on the pattern.

The large variability in the mean swimming speed of adult seals cannot be captured with a single fixed value. In consequence, for the future evolution of this movement model into a population model targeted at predicting seal population dynamics, a probability distribution for the *mean-speed-adults* parameter may be implemented. We thus developed the probability distribution based on re-calibration results and observed field data to account for such individual variability (see Appendix E). Morales et al. (2004) suggested a similar approach for their elk (*Cervus elaphus*) movement model, which was also developed with a small data set. Ultimately, the probability distribution of seal movement speed should be obtained from as many individuals as possible to improve model fit and to overcome the issue caused by large intraspecific variation. In addition, identification of the factors influencing seal spatial behaviour would be beneficial.

Seals are highly cognitive mammals and their behaviour is likely affected by many processes that we cannot identify using telemetry data alone. Using simple movement data for calibrating a model of such cognitively competent animals living in highly heterogeneous environment is challenging. Morales et al. (2004) observed that simple correlated random walk based movement model is too simple for predicting elk movements. Better match to observed datasets was achieved with a model that included multiple movement states, i.e. multiple correlated random walks that each have different parameter distributions. Our model would benefit if more information on seal behaviour could be connected to observed individual characteristics or environmental factors. For the future development of our Saimaa ringed seal model, it would be beneficial to identify these seal behavioural states, which could be then implemented in the model, thus improving the fit. Identifying individual movement patterns and the motivation behind them, would also benefit movement ecology study in general as this aspect is neglected in many cases (Holyoak et al., 2008).

4.3. Model sensitivity

The mean swimming speed had the strongest influence on the distance moved by adult seal from the initial position and thus on the size of its home range. On the other hand, exhaustion rate was the main and basically the only driver of the time passed between haul outs. The quicker the seal gets exhausted, the less time it spends foraging before needing to rest on a haul out site.

In addition to seal-related parameters, we estimated the sensitivity of movement patterns to environmental factors. The higher number of haul out sites we implement in the model, the greater is the simulated distance from home and the shorter are the time periods that seals move between consecutive haul out events. Site selection is partly based on distance to the visited sites, which explains the effect of the number of haul out sites on movement patterns to some extent. Furthermore, increasing the availability of haul out sites increases the probability that the seal has a rest even if it is not exhausted. Consequently, the time spent foraging between consecutive haul out events shortens.

Moreover, the selection of haul out sites and foraging areas used during the warm-up period increases variation between model replicates. The model is run for 12.5 months before collecting the results, so the seal develops a memory of certain foraging areas and resting sites that are selected in a random way, thus introducing variability among model runs.

4.4. Model application and outlook

This paper describes a model predicting Saimaa ringed seal movement behaviour. We started with a simple hypothesis, where we assumed the complexity of the landscape would explain the variation in home range size among the individuals. However, the differences in the landscape were not sufficient to explain the observed movement patterns. Therefore, the model would benefit from further variables, adding some more biological and environmental aspects that affect seal behaviour. More studies are needed to find the underlying mechanisms of the observed movement patterns. However, the current model version forms a sound basis for further development. Ultimate implementation of seals' full life cycle and interactions between individuals in the model would enable the analysis of population dynamics under changing environmental conditions and conservation and management scenarios. One of the major factors causing mortality in Saimaa ringed seals is bycatch in gillnet fishing (Kovacs et al., 2012); therefore, fishing restrictions have been applied in the most important breeding areas. Despite these restrictions, bycatch mortality has remained relatively high (Auttila, 2015; Kunnasranta et al., 2016), and therefore, there is a demand to extend the restrictions both temporally and spatially. Although, the current model version has to be considered preliminary, and several improvements could be considered, an application of the model could be used to study the effects of different fishing restriction scenarios, which would provide much needed information on the effectiveness of mitigation methods.

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Appendix A: TRACE document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that our model presented in:

> **Liukkonen, L., Ayllón, D., Kunnasranta, M., Niemi, M., Nabe-Nielsen, J., Grimm, V., Nyman, A.-M., 2017. Modelling movements of Saimaa ringed seals using an individual-based approach. Ecological Modelling.**

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

> Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25: 479-486.

and uses the updated standard terminology and document structure in:

> Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Kułakowska K, Liu C, Martin BT, Meli M, Radchuk V, Schmolke A, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling*

and

> Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecological Modelling*.

If this document include **hyperlinks**, navigation back and forth along previously chosen links works via "ALT" + "←" or "ALT" + "→".

Contents

1 Problem formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

Summary:

The Saimaa ringed seal movement model enables the study of mechanisms affecting seal movement behaviour. Moreover, this model version serves as a sound base for further development into a seal population model. Ultimately, the population model could be utilised in assessing the effects of greatly debated mitigation methods on seal population dynamics.

Saimaa ringed seal (*Phoca hispida saimensis*) is a subspecies of ringed seal (*Phoca hispida*) endemic to Lake Saimaa. The current population size of this endangered subspecies is around 350 individuals (Liukko et al., 2016; Metsähallitus, 2016). Seal's ecology have been studied in several field studies (Auttila, 2015; Kunnasranta, 2001; Niemi, 2013; Sipilä, 2003; Valtonen, 2014) and many of the findings have been utilised in development of conservation measures, which are essential in preventing extinction of Saimaa ringed seal. However, field studies are expensive and difficult to conduct, especially as the species of research is rare and endangered. Therefore, we analysed the existing telemetry datasets and developed this Saimaa ringed seal movement model to serve as a tool for studying seal ecology and utilise the information in development of more effective conservation methods.

The proximate purpose is to model movements of adult Saimaa ringed seals, and to find possible mechanisms for home range formation. This would facilitate better understanding of seal ecology and the information could be utilised in seal conservation. The ultimate goal is to develop the model further into a seal population model, which would enable assessing the efficacy of current conservation measures, especially the fishing restrictions. One of the main threats for the population is bycatch in gillnet fishing (Niemi et al., 2013b). Therefore, fishing closures have been applied in the main breeding areas in springtime and early summer, and some other types of fishing gear are banned throughout the year. However, despite the closures, bycatch mortality has remained high (Metsähallitus, 2011, 2012, 2013, 2014, 2015, 2016), and therefore, there is need to extend the restrictions both spatially and temporally. Ultimately, the model would enable assessing the effects of varying temporal and spatial fishing closures on the population dynamics. This is critical, as the conservation methods face strong criticism (Tonder and Jurvelius, 2004), and therefore, mitigation methods must be assessed thoroughly while taking all the stakeholders into account.

Seal movement behaviour is assessed measuring *distance from home* and *time between haulouts* output variables. In model runs home refers to the site where seal is initialised and in the field data it refers to the capture site. These output variables are used for comparing model outputs to the patterns observed in field studies. In addition, coordinates of the seal movement can be recorded and used in calculating home range size for the simulated animal.

2 Model description

This TRACE element provides supporting information on: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

Summary:

> **Here, we present the model description which follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006; Grimm et al., 2010).**

2.1 Purpose

The purpose of the model is to simulate seal movement patterns based on assumptions regarding resting and foraging behaviour.

2.2 Entities, state variables, and scales

The area represented in the model (Haukivesi and Joutenvesi basins) is 762 km^2. The model world consists of a grid of 1000 x 1000 square grid cells, or patches; each patch represents an area of 0.00297 km^2 (54.5 m x 54.5 m). Model entities are habitat patches, seal and rock agents. Habitat patches are either land or water patches (land?; true/false). Some of the land patches were further characterized as island patches (island?; true/false). Land areas larger than 0.01 km^2 and less than 2.98 km^2 are considered as islands in the model. The minimum size of an island preferred for haul out is reported to be 0.0002 km^2 (Niemi et al., 2013a) but was increased to 0.01 km^2 in the model to keep the habitat as realistic as possible while taking into account the limited resolution of the map. Water patches are divided into three categories: Deep water (≥ 15 m), shallow water (< 15 m) (deep; true/false), and water suitable for haul out sites (stone-place?; true/false). These are water patches next to islands where rocks are created, as such areas are regarded as suitable haul out sites. The amount of potential haul out sites in nature is unknown and was thus estimated from haul out data and home range sizes. Observed average number (N=13) of haul out sites per seal per average home range size was extrapolated to the study area. Consequently, a total of 121 haul out sites were randomly created at initialization; the site that was determined as the starting point for the seal was characterized only by its coordinates (init-site; x: 0–1000, y: 0–1000). Seals are characterized by their age (age-in-months; 48 months), exhaustion level (exhaustion; 0.1–0.999), movement variables, including distance travelled (step-length; 0.1– metres) and direction (turning-angle; 0–360 degrees), and memory variables, including spatial memory of haul out sites and deep water areas (stone-cors; 0–100 sites, deep-cors; 0–100 sites), and the memory value of each visited haul out site (memory-stones-list; 0.1^{-7}–0.99). Only one seal is simulated at a time.

The time step is 20 minutes when the seal is swimming and 60 minutes when it is hauled out. This matches the resolution of data recorded with GPS/GSM tags. The ice-covered season (January–March) is omitted, as seals are moving in a smaller area within their home range (Kelly et al., 2010). The simulation starts at the beginning of April and is first run for 12.5 months; during the last 0.5 months of this period, the seal has its initial site as the only target for haul out. This warm-up period enables the seal to have some haul out sites and deep water areas in its memory before the actual data collection begins in the middle of consecutive April when the warm-up period of 12.5 months have passed. Results were then recorded after this warm-up period for duration of 4.17 months for individual ER11 and 5.96 months for the rest of the individuals.

2.3 Process overview and scheduling

The processes described below are executed in the same order in each time step (Fig. A.1). Here, only summary descriptions of the processes are provided; see section 2.4.7 (Submodels) for details. Submodel names are given in italics:

(1) *Update time step* – Length of time step is updated, depending on the seal's activity.

(2) *Update age* – Seal's age (in months) is updated. Ice-covered season (January–March) is skipped by adding 3 months to seal's age.

(3) *List coordinates* – Coordinates of the seal's locations are updated for home range calculations.

(4) *Decay memory* – Memory values of the visited haul out sites are updated as memory decays over time.

(5) *Remember haul outs* – If the seal is currently hauled out, the site is added to memory.

(6) *Rest* – If the seal's exhaustion is above the moving threshold, it rests. The seal starts moving again when exhaustion decreases below the moving threshold. Movement mode is set to 1 (sets a deep water target patch) if there are deep water patches in the seal's memory and to mode 2 (correlated random walk) if there are not. Based on initial model results, we implemented an alternative assumption that resting occurs not only when the seal is exhausted but also when there is a haul out site nearby.

(7) *Move* – There are three different movement modes: movement to a previously visited deep water patch (mode 1), correlated random walk (mode 2), and movement towards a haul out site (mode 3).

(8) *Write results/Update plots* – Output files are written, and plots are updated.

Fig. A.1 A simple flow diagram of processes in the Saimaa ringed seal movement model. Processes in the middle box are performed with each time step; depending on the movement mode, different additional procedures are executed. Boxes with dashed lines indicate the state criteria when the movement mode is switched.

2.4 Design concepts

The design concepts *Interaction* and *Collectives* do not apply to this model. *Adaptation*, *Objectives*, and *Prediction* are represented implicitly in the imposed haul out behaviour.

Basic principles – The emergence of home ranges within existing IBMs is resource– or movement/memory–based. In the former case (e.g. Carter et al., 2015; Wang and Grimm, 2007), animals add area to their home range until they have secured sufficient resources. In the latter (Nabe-Nielsen et al., 2013; Van Moorter et al., 2009), animals move while foraging but tend to return to sites they memorize as being preferable. Our model is movement/memory-based: seals remember visited haul out sites and foraging areas to some extent, which also influences space use. Furthermore, we implicitly represent bioenergetics as exhaustion, which requires haul out and increases with foraging time.

Emergence – Movement patterns, in terms of area used and time spent either moving or hauled out, emerge partly because of animal personalities in reality. Hence, in the model, different personalities appear as different speed parameter values. Furthermore, the capacity and permanence of the seal's memory of visited haul out sites and foraging areas plays a role in the emergence of movement patterns. In addition, the location and number of potential haul out sites in the area affect seal movements in the model.

Learning – Seals learn about their habitat by remembering visited haul out sites and deep water grid cells.

Sensing – The seal senses and avoids land in its moving direction. It also senses if it is in a deep water area or if there is a haul out site nearby, and it knows the distance to visited haul out rocks.

Stochasticity – Step length in all movement modes and moving direction in movement mode 2 (correlated random walk) are drawn from truncated normal distributions. In addition, the positions of haul out sites are randomly assigned at initialization. Furthermore, haul out sites and deep water foraging areas that seals use may differ among replicates; this introduces another factor creating stochasticity.

Observation – Position, distance from home (km), movement duration (h), and duration of haul outs (h) are measured every time step. Home refers to the location where the seal is initialized.

2.5 Initialization

The world is created by importing GIS shape files for water, deep water (≥15 m) and land areas. A total of 121 haul out rocks are randomly created near islands. One seal is created and positioned on a user-defined haul out site, set to resting mode, and given an empty memory except for the current haul out site, an exhaustion of 0.998 (maximum exhaustion 0.999) and an age of three months.

2.6 Input data

The model does not include input of data representing time-varying environmental drivers.

2.7 Submodels

Model parameters are listed in Table A.1.

2.6.1 Update time step, age and time

The time step is set to 20 minutes if the seal is moving and to 60 minutes if it is hauled out. Age and current time are updated accordingly and rescaled to months.

2.6.2 List coordinates

Coordinates of the seal's location are stored in a list for home range estimations. Because the time step is three times longer (60 min) when hauled out, every pair of haul out sites' coordinates are listed three times to avoid bias in the results by emphasizing relocations when moving. In addition, only 25% of movement coordinates are listed to match the resolution of telemetry data. GPS/GSM tags fail to connect to the satellites occasionally, and therefore, the locations may not be obtained every 20 minutes as programmed.

2.6.3 Decay memory

Seals remember visited haul out sites. However, the memory decays over time (i.e., seals forget). The last haul out site on the list will be removed if there are already 100 sites in the memory or if the memory value for a site is < 10^{-8}. Memory decay is represented according to Nabe-Nielsen et al. (2013):

$$M[c]_{t+1} = M[c]_t - (M_R \times M[c]_t \times (1 - M[c]_t)) \,,$$

where t is time in units of time steps, $M[c]$ is the memory of a location c (unitless), and M_R is the reference memory decay rate (1/h).

2.6.4 Remembering haul outs

If the seal is hauled out, the site is added to its memory and given a memory value of 0.99. In cases where the site is already in the seal's memory, the entry representing the earlier visit is removed.

2.6.5 Rest

If the seal is hauled out or sleeping in water, exhaustion decreases following:

$$E[c]_{t+1} = E[c]_t - (R_R \times E[c]_t \times (1 - \frac{E[c]_t}{E[c]_{max}})) ,$$

where t is time, $E[c]$ is the exhaustion level, $E[c]_{\max}$ is the maximum of exhaustion level, and R_R is the exhaustion recovery rate. If exhaustion falls below the moving threshold, the exhaustion level is set to 0.1 and either movement mode 1 or 2 is selected (see below for definition of movement modes).

2.6.6.1 Move

2.6.6.1.1 Movement modes

There are three movement modes that seals can perform. After hauling out (during which movement mode is *false*), seals head to a deep water area to forage (mode 1); having reached the target deep water grid cell, they start moving by correlated random walk (mode 2). After foraging, seals head back to the haul out sites to rest (mode 3). The choice between these three movement modes is based on the state variable *exhaustion*. When the seal is hauled out, its level of exhaustion decreases; once it decreases low enough to reach the *moving threshold*, either movement mode 1 or 2 is set. The seal either heads to an earlier visited deep water area (mode 1) or starts moving by correlated random walk (mode 2) if it has not visited any deep water areas yet (e.g., at the initialization of the model). Once a deep water area is reached, movement mode 2 is set (provided that the seal was not in mode 2 already). When *exhaustion* reaches the level of parameter *exhaustion threshold*, movement mode 3 is selected and the seal goes to a haul out site to rest (haul out submodel 1: haul-out-by-exhaustion) and the movement mode is set to *false*. If *exhaustion* exceeds its maximum value before reaching a haul out site, the seal sleeps in water until exhaustion decreases low enough and it starts moving again. The *sleep in water* procedure is not possible in deep water. We also tested an alternative structure regarding haul out behaviour, where movement mode 3 is not only selected when a seal is exhausted but also when the seal's *exhaustion* exceeds the parameter *exhaustion-ho-limit* and there is a haul out site within distance of the parameter *ho-distance* (haul out submodel 2: haul-out-by-exhaustion-and-closeness).

The following processes are common to all movement modes and are performed before moving in the order listed:

(1) *Adjust step length* – Step length is drawn from a normal distribution with its mean set to the parameter *mean-speed-adults* and its standard deviation to *sd-speed-adults*. Minimum step length is set to 0.1 to avoid seals moving backwards.

(2) *Adjust turning angle* – Turning angle is drawn from a normal distribution with its mean set to the parameter *mean-turning* and its standard deviation to *sd-turning*.

(3) *Set exhaustion rate* – Exhaustion rate is set to the value of parameter *exhaustion-rate-adults.*

(4) *Update exhaustion level* – Exhaustion level increases in every movement step according to:

$$E[c]_{t+1} = E[c]_t + \left(Exh_R \times E[c]_t \times \left(1 - \frac{E[c]_t}{E[c]_{max}}\right)\right),$$

where Exh_R is the exhaustion rate, and E[c] is the exhaustion level (unitless).

(5) *Remember deep* – If the seal is in a deep water patch, the patch is added to the seal's memory. Earlier visits to that patch are removed from the memory. If a target deep water patch is within the step length or a shorter distance, the seal moves there.

2.6.6.1.2 Targeted vs. non-targeted moves
Earlier described movement modes can be further divided into targeted and non-targeted moving. In *non-targeted moving*, the seal moves by correlated random walk (mode 2). The turning angle is updated every time step, land is avoided if necessary, and a step is taken forward. Whereas in *targeted moving*, movement is directed either towards a deep water foraging area (mode 1) or a haul out site (mode 3). If the seal is moving towards a deep water area, one deep water grid cell is randomly selected from the seal's memory and set as a target. The selection of the target haul out site is based on the distance from the seal's position and time when the seal last visited that site, as described below.

Calculate haul out site attraction value – Target haul out site is chosen by calculating the attraction values of previously visited haul out sites as follows:

$$A\,[c]_t = \frac{1}{M\,[c]_t} \times D\,[c]_t$$

where A [c] is the attraction value of the site, M [c] is the memory value of the site (see submodel *decay-memory*), and D [c] is the distance of visited haul out sites to the seal. The haul out site with the smallest value is chosen as a target.

2.6.6.1.3 Avoid land
The design of the land avoidance procedure was inspired by a green turtle model by Dalleau (2013). A flow diagram of the procedure is presented in Figure A.2. Land avoidance mode is set off if there is no land ahead and the difference from the current heading to the target is ≤ 45 degrees. This submodel consists of four different procedures:

(1) *See if there is land ahead* – The seal checks if there is land ahead within one step length or less. Distances smaller than one step length are needed to avoid the seal jumping over narrow land areas.

(2) *Avoid land decision* – Land avoidance direction selection, i.e., left or right, is based on two steps. First, the seal turns 45 degrees left and right and calculates which turning direction has less land within an angle of 90 degrees and a radius defined by the parameter *land-distance*. If there is an equal amount of land in both directions, the moving direction is chosen randomly.

(3) *Avoid land right* – First, the seal checks if there is land ahead in its moving direction (*see if land ahead*). If not, the seal turns counter-clockwise in steps of 10 degrees until it detects land in its moving direction. Then, the seal chooses the previous turning direction and takes a step forward. This makes the seal follow the shoreline of an island. If there was land ahead at the beginning of this procedure, the seal will avoid it from the right side. It turns clockwise in steps of 10 degrees until there is no land ahead and then takes a step forward. If the seal has already turned 360 degrees and has not encountered land, it takes a step towards the set target. Sometimes the step length is long enough to make the seal encounter land in every direction. In such case, step length is reduced by 50% and the land avoidance procedure is repeated.

(4) *Avoid land left* – This procedure is identical to *avoid land right*, except that the seal turns clockwise if there is no land in its moving direction and counter-clockwise if there is. This makes the seal avoid land from the left side.

2.6.7 Write results/Update plots
The output variables *distance from home* and *moving duration*, and additionally coordinates of seal movements for home range estimations are written into an output file. Plots of the

seal's distance from home, moving duration and haul out duration are updated every time step.

Fig. A.2 Flow diagram of land avoidance decision-making in the Saimaa ringed seal movement model.

3 Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary:

> **Data of GPS/GSM tracked Saimaa ringed seals were used in model parameterization. Design of the overall model structure was guided by current knowledge on seal ecology.**

Adult Saimaa ringed seals have home ranges of 92 km^2 on average (Niemi et al., 2012), which is remarkably smaller than home ranges reported in other ringed seal subspecies (e.g. Born et al., 2004; Oksanen et al., 2015). In addition to compact home ranges, seals' sedentary behaviour is supported by strong evidence of annual and interannual site fidelity for haul out sites, which are mainly used for moulting and resting (Koivuniemi et al., 2016; Koskela et al., 2002; Kunnasranta, 2001; Niemi et al., 2013a). Haul out takes place in snow lairs in winter time; as weather gets warmer in the spring, lairs collapse and seals start to haul out first on the ice, and later on terrestrial platforms, typically rocks located on the shoreline of small islands, but not in the vicinity of the mainland (Niemi et al., 2013a). According to telemetry studies (Niemi et al., 2013a), Saimaa ringed seals have an average of 13 haul out sites during the open water season. Haul out takes over half of seals' time during the moulting period from late April to early June, with activity peaking in the afternoon when the temperature is highest, which is reported to be beneficial for moulting (Boily, 1995; Paterson et al., 2012). During pre- and post-moulting periods, haul out takes no more than 20% of total time (Hyvärinen et al., 1995; Kunnasranta, 2001; Niemi et al., 2013a) and is mainly nocturnal. Night time haul out has been suggested to be an adaptation to prey fish behaviour and disturbance, which is more frequent during the day (Hyvärinen et al., 1995; Kunnasranta, 2001; Kunnasranta et al., 2002; Niemi et al., 2013a).

Haul out is affected by many factors, such as weather (i.e., amount of solar radiation, wind, temperature and cloud cover), physiological status, and possible disturbance (Carlens et al., 2006; Moulton et al., 2005; Moulton et al., 2002; Niemi et al., 2013a). Especially in the case of the Saimaa ringed seal, disturbance by humans is an important factor affecting haul out, as the lake is a popular place for recreational activities. Occasionally, seals are forced to escape to water when hauled out, as they are approached by human visitors either intentionally or unintentionally (Niemi et al., 2013a). In addition to terrestrial sites, resting can also take place in water. Seals have been observed to make consecutive long duration dives that are suggested to be associated with resting (Hyvärinen et al., 1995; Kunnasranta et al., 2002). These so-called sleeping dives usually take place next to haul out sites and are more likely to occur when the weather is not optimal for haul out, e.g., when it is raining (Kunnasranta et al., 2002). Still, even though resting is possible in water, haul out remains an important part of a seal's daily activities throughout the year, with a peak centred around the breeding and moulting seasons.

There is seasonal variation in Saimaa ringed seal feeding patterns. Seals' feeding activity is reduced during spring due to the breeding, nursing and moulting seasons. In late summer, seals need to forage actively to gain weight for the upcoming winter, as blubber is needed to provide protection from harsh thermal conditions. Seals are generalists that feed mainly on small schooling fish species, such as perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), vendace (*Coregonus albula*), smelt (*Osmerus eperlanus*) and ruff (*Gymnocephalus cernuus*) (Auttila et al., 2015; Kunnasranta et al., 1999). Adult seals prefer deep water foraging areas, where vendace and smelt, that are rich in fat content, are mainly found outside spawning season (Kunnasranta et al., 1999). Other prey species are abundant in shallow areas throughout the year, and therefore seal foraging is not only limited to deep-water areas. The quantity of prey fishes is classified as medium to very high for perch and smelt in northern parts of the lake (Valkeajärvi et al., 2010). Therefore, food is not currently considered to be a limited resource (Auvinen et al., 2005).

We based the model on simplifying assumption that seal movements consist of cycles of foraging in deep water areas and resting on haul out sites next to small islands. Movements are based on both correlated random walks and unidirectional movements towards foraging areas and haul out sites. To get simulated seals to return to previously used haul out and foraging areas, we implemented a spatial memory component (Nabe-Nielsen et al., 2013). This addition of memory enables the formation of home ranges.

The model was developed, parameterized and tested following the pattern-oriented framework (Grimm and Railsback, 2012; Grimm et al., 2005). Data used in the model development were obtained by equipping seals with GPS/GSM tags (Sea Mammal Research Unit, St. Andrews University, UK) during the annual moulting seasons in Hauki- and Joutenvesi regions in

2007-2011. In addition to record dive data (depth, duration), tags were set to determine the position every 20 minutes if the seal was in the water and every 60 minutes if it was hauled out. A seal was considered to be hauled out if the wet/dry sensor on the tag had been dry for 10 minutes; the haul out was considered to have ended when the sensor had been wet for 40 seconds. We used two patterns in the model parameterization and testing; *distance from home* and *moving duration*. *Distance from home* describes the extent of seal movements from the initial site in the model runs, or, from the capture site in telemetry data. *Moving duration* is the time that seal spends foraging between consecutive haul out events. Model development took place in two distinct phases. In the first phase of model development and parameterization, GPS-telemetry data from one adult male (ER11; 3822 relocations, tracking duration 125 days) from the study area were used to develop and calibrate the model. This individual had the highest resolution data in the database (Saimaa ringed seal telemetry database, University of Eastern Finland 2015). In the second phase, additional data from five individuals (HE07♀: 3003 relocations, 191 d; KJ07♂: 4475 relocations, 218 d; OL10♀: 2155, 180 d; TO09♂: 3254 relocations, 194 d; and VI09♂: 4618 relocations, 199 d) were used for model validation and final calibration of one parameter. All data were limited to the open water season and constrained to the same temporal resolution as the shortest tracking period, except for individual ER11, whose data were fully used. AdehabitatLT package (Calenge, 2011) in R (R Development Core Team, 2011) was used for calibration. Additionally, datasets of 18 seals were used to develop probability distribution for the speed parameter (see Chapter 6, model output verification). These datasets were not used in model calibration.

4 Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary:

The simplifying assumptions in the model design are discussed here.

Since there is only one seal individual, the model lacks intra- and interspecific interactions. For example Ladoga ringed seals are known to form groups, e.g. when hauling out (Kunnasranta et al., 1996; Sipilä et al., 1996). However, Saimaa ringed seals are rather solitary and no strong intraspecific interaction has been observed. This could be related to the fact that there are only around 350 individuals left, and due to the small population size, interactions do not occur. Therefore, the lack of intraspecific interaction in the model is not considered to have a significant effect on the model outputs. In addition to ignorance to intraspecific interactions, interspecific interaction were not taken into account. The most important interspecific interaction would be between seals and humans. There are summer cottages on the shores and many recreational activities take place on Lake Saimaa. Therefore, the disturbance caused by humans must have an effect on seals behavior and space use but the extent is not fully known. It has been observed that occasionally seals are forced to escape to water when hauling out as human visitors approach the haulout site (Niemi et al., 2013a).

Model's temporal scale lacks the winter months, i.e. the times when there is ice cover on Lake Saimaa and seals are moving in a smaller area within their home range (Kelly et al., 2010). Ignorance of the ice covered season justified because the ultimate purpose of this project is to study the effects of gill net fishing on seal population dynamics, and the peak in bycatch mortality takes places on open water season in spring and summer time (Niemi et al., 2013b).

Furthermore, the movement in the model highly simplified. Seal only moves between foraging areas (deep water) and haulout sites. Movement between these two sites is rather straightforward; it is only on the foraging areas where seal moves according to correlated random walk. In addition, the land avoidance implemented in the model is based only on the amount of land seal can sense on its right and left side. In real system, there are undoubtedly many other factors affecting seals decision making when avoiding land and deciding which routes to take.

The selection of haulout sites and foraging areas is also simplified. Haulout sites are chosen based on distance to the site and time, since the seal visited there last time. Foraging areas are determined by choosing random deep-water patch from seal's memory. These processes are much more complex in nature, but in the current version, accuracy is enough for the objective of the model. Also, the duration of haulout is simplified as the only factors affecting are the state of exhaustion in the beginning of haulout and the rate at which exhaustion decreases. In real environment haulout is affected, e.g. by weather, physiological status of the seal and possible disturbance (Carlens et al., 2006; Moulton et al., 2005; Moulton et al., 2002; Niemi et al., 2013a)

5 Implementation verification

This TRACE element provides supporting information on: (1) whether the computer code for implementing the model has been thoroughly tested for programming errors and (2) whether the implemented model performs as indicated by the model description.

Summary:

> **The program was tested with several debugging elements. Many of them were purely visual while programming, but some more elaborate methods were also used to test the code.**

Testing was performed in a simplified model environment (Figure A.3) without using a map of the real study environment.

Fig. A.3 A simplified model environment was used to detect bugs in the code and test the model performance. Light blue = shallow water, dark blue = deep water, green = island, black circles = haulout sites

Tested processes and description of the testing methods

(1) Seal swims only in water, not land.

If seal ends up on land, an error message is displayed and seal is moved to closest water patch.

(2) Exhaustion is in the range of 0 to 1

If value for variable *exhaustion* exceeds 1.000, it is set to 0.999 every time step.

(3) Time increment

Model was run, output file was written and imported to Excel. Time increment every time step was calculated and confirmed to be 60 min when seal was hauling out and 20 min when moving (Fig. A.4).

ticks	time	change in tir	age-in-months of seals	to-hours-sca	step-taken of seals	SEE CONCLUSIONS
738	1.025	1	1.025	1	0	
739	1.026388889	1	1.026388889	1	0.1	<-- End of haul out
740	1.026851852	0.333333333	1.026851852	3	1.495017659	
741	1.027314815	0.333333333	1.027314815	3	3.665600696	
742	1.027777778	0.333333333	1.027777778	3	2.671193817	
743	1.028240741	0.333333333	1.028240741	3	1.164365166	
744	1.028703704	0.333333333	1.028703704	3	4.045374868	
745	1.029166667	0.333333333	1.029166667	3	2.828427125	
746	1.030555556	1	1.030555556	1	0	
747	1.031944444	1	1.031944444	1	0	
748	1.033333333	1	1.033333333	1	0	
749	1.034722222	1	1.034722222	1	0	
750	1.036111111	1	1.036111111	1	0	
751	1.0375	1	1.0375	1	0	
752	1.038888889	1	1.038888889	1	0	
753	1.040277778	1	1.040277778	1	0	
754	1.041666667	1	1.041666667	1	0	
755	1.043055556	1	1.043055556	1	0	
756	1.044444444	1	1.044444444	1	0	
757	1.045833333	1	1.045833333	1	0	
758	1.047222222	1	1.047222222	1	0	
759	1.048611111	1	1.048611111	1	0	
760	1.05	1	1.05	1	0	
761	1.051388889	1	1.051388889	1	0	
762	1.052777778	1	1.052777778	1	0	
763	1.054166667	1	1.054166667	1	0	
764	1.055555556	1	1.055555556	1	0	
765	1.056944444	1	1.056944444	1	2.079942471	<-- End of haul out

Fig. A.4 Output file of model simulation showing that when seal is hauling out (step taken = 0) time step is 60 min (change in time = 1 h), and when seal is moving (step taken > 0) time step is 20 min (change in time = 0.333333333 h)

(4) Increase and decrease of exhaustion

Equation for increment and decrement of exhaustion were implemented in both NetLogo and Excel and the difference was calculated and confirmed to be 0 (Fig. A.5).

time [month	time [hours]	exhaustion NetLogo	exhaustion Excel	difference Netlogo - Excel	movement-mode
4.44	3197.67	0.1187	0.1187	0.0000	1
4.44	3198.00	0.1292	0.1292	0.0000	1
4.44	3198.33	0.1404	0.1404	0.0000	1
4.44	3198.67	0.1525	0.1525	0.0000	1
4.44	3199.00	0.1654	0.1654	0.0000	1
4.44	3199.33	0.1792	0.1792	0.0000	2
4.44	3199.67	0.1939	0.1939	0.0000	2
4.44	3200.00	0.2096	0.2096	0.0000	2
4.44	3200.33	0.2261	0.2261	0.0000	2
4.45	3200.67	0.2436	0.2436	0.0000	2
4.45	3201.00	0.2621	0.2621	0.0000	2
4.45	3201.33	0.2814	0.2814	0.0000	2
4.45	3201.67	0.3016	0.3016	0.0000	2
4.45	3202.00	0.3227	0.3227	0.0000	2
4.45	3202.33	0.3445	0.3445	0.0000	2
4.45	3202.67	0.3671	0.3671	0.0000	2
4.45	3203.00	0.3904	0.3904	0.0000	2
4.45	3203.33	0.4142	0.4142	0.0000	2
4.45	3203.67	0.4384	0.4384	0.0000	2
4.45	3204.00	0.4630	0.4630	0.0000	2
4.45	3204.33	0.4879	0.4879	0.0000	2
4.45	3204.67	0.5129	0.5129	0.0000	3
4.45	3205.00	0.5379	0.5379	0.0000	3
4.45	3205.33	0.5627	0.5627	0.0000	3
4.45	3205.67	0.5873	0.5873	0.0000	3
4.45	3206.00	0.6116	0.6116	0.0000	3
4.45	3206.33	0.4928	0.4928	0.0000	FALSE
4.45	3207.33	0.3678	0.3678	0.0000	FALSE
4.46	3208.33	0.2516	0.2516	0.0000	FALSE
4.46	3209.33	0.1574	0.1574	0.0000	FALSE

Fig. A.5 Seal exhaustion levels imported from model simulation, and exhaustion levels calculated in Excel. Differences of these values are all 0, therefore, we can conclude that implementation of exhaustion increase/decrease is correct.

(5) Movement mode in relation to exhaustion level

It was verified that exhaustion level increases when seal is moving and decreases when it is hauling out, and the movement mode is correctly switched based on the exhaustion values. This was done by writing an output file from model run and importing it to Excel and comparing the exhaustion values and movement modes (Fig. A.6)

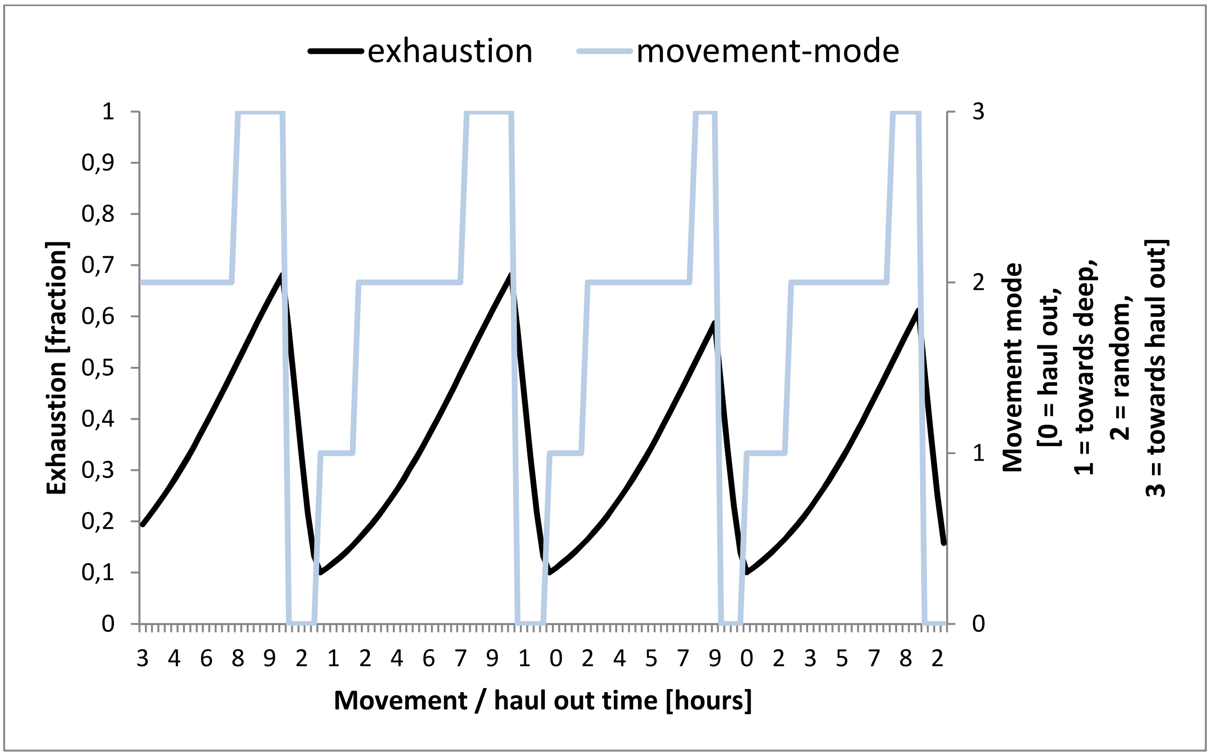

Fig. A.6 Movement modes and exhaustion levels during a model simulation.

(6) Memory

Each haul out site seal visits is added to its memory and the memory decays over time. Addition of haul out sites to memory and the decrease of memory value was tested comparing the values exported from the model to calculations performed in Excel. The difference between values obtained from the model and Excel implementation was 0 (Fig. A.7). Therefore, we can conclude that the implementation is correct. After haul out event seal determines earlier visited deep water area as a target and goes there foraging. It was also verified in Excel that this target determination is implemented correctly in the model (Fig. A.8).

10000	10000	memory-stones-list of seals (NetLogo)								memory decrease excel							
time	movement-mode																
7.394	FALSE	0.9900	**0.9897**	0.9890	0.9883	0.9871	0.9859	0.9840	0.9799								
7.395	FALSE	0.9900	0.9897	0.9890	0.9882	0.9871	0.9859	0.9840	0.9799								
7.396	FALSE	0.9900	0.9897	0.9890	0.9882	0.9871	0.9859	0.9839	0.9799								
7.398	1	0.9900	0.9897	0.9890	0.9882	0.9871	0.9859	0.9839	0.9798								
7.398	1	**0.990**	**0.990**	**0.989**	**0.988**	**0.987**	**0.986**	**0.984**	**0.980**	**0.990**	**0.990**	**0.989**	**0.988**	**0.987**	**0.986**	**0.984**	**0.980**
7.399	1	0.9900	0.9897	0.9889	0.9882	0.9871	0.9859	0.9839	0.9798	0.99	0.9897	0.9889	0.9882	0.9871	0.9859	0.9839	0.9798
7.399	1	0.9900	0.9897	0.9889	0.9882	0.9871	0.9859	0.9839	0.9798	0.99	0.9897	0.9889	0.9882	0.9871	0.9859	0.9839	0.9798
7.400	2	0.9900	0.9897	0.9889	0.9882	0.9871	0.9858	0.9839	0.9798	0.99	0.9897	0.9889	0.9882	0.9871	0.9858	0.9839	0.9798
7.400	2	0.9900	0.9896	0.9889	0.9882	0.9870	0.9858	0.9838	0.9797	0.99	0.9896	0.9889	0.9882	0.987	0.9858	0.9838	0.9797
7.400	2	0.9900	0.9896	0.9889	0.9881	0.9870	0.9858	0.9838	0.9797	0.99	0.9896	0.9889	0.9881	0.987	0.9858	0.9838	0.9797
7.401	2	0.9899	0.9896	0.9889	0.9881	0.9870	0.9858	0.9838	0.9797	0.9899	0.9896	0.9889	0.9881	0.987	0.9858	0.9838	0.9797
7.401	2	0.9899	0.9896	0.9889	0.9881	0.9870	0.9858	0.9838	0.9797	0.9899	0.9896	0.9889	0.9881	0.987	0.9858	0.9838	0.9797
7.402	2	0.9899	0.9896	0.9889	0.9881	0.9870	0.9858	0.9838	0.9797	0.9899	0.9896	0.9889	0.9881	0.987	0.9858	0.9838	0.9797
7.402	2	0.9899	0.9896	0.9889	0.9881	0.9870	0.9858	0.9838	0.9796	0.9899	0.9896	0.9889	0.9881	0.987	0.9858	0.9838	0.9796
7.403	2	0.9899	0.9896	0.9888	0.9881	0.9870	0.9857	0.9838	0.9796	0.9899	0.9896	0.9888	0.9881	0.987	0.9857	0.9838	0.9796
7.403	2	0.9899	0.9896	0.9888	0.9881	0.9870	0.9857	0.9837	0.9796	0.9899	0.9896	0.9888	0.9881	0.987	0.9857	0.9837	0.9796
7.404	2	0.9899	0.9896	0.9888	0.9881	0.9869	0.9857	0.9837	0.9796	0.9899	0.9896	0.9888	0.9881	0.9869	0.9857	0.9837	0.9796
7.404	2	0.9899	0.9896	0.9888	0.9881	0.9869	0.9857	0.9837	0.9796	0.9899	0.9896	0.9888	0.9881	0.9869	0.9857	0.9837	0.9796
7.405	2	0.9899	0.9895	0.9888	0.9880	0.9869	0.9857	0.9837	0.9795	0.9899	0.9895	0.9888	0.988	0.9869	0.9857	0.9837	0.9795
7.405	2	0.9899	0.9895	0.9888	0.9880	0.9869	0.9857	0.9837	0.9795	0.9899	0.9895	0.9888	0.988	0.9869	0.9857	0.9837	0.9795
7.406	2	0.9898	0.9895	0.9888	0.9880	0.9869	0.9857	0.9837	0.9795	0.9898	0.9895	0.9888	0.988	0.9869	0.9857	0.9837	0.9795
7.406	2	0.9898	0.9895	0.9888	0.9880	0.9869	0.9856	0.9836	0.9795	0.9898	0.9895	0.9888	0.988	0.9869	0.9856	0.9836	0.9795
7.406	2	0.9898	0.9895	0.9888	0.9880	0.9869	0.9856	0.9836	0.9795	0.9898	0.9895	0.9888	0.988	0.9869	0.9856	0.9836	0.9795
7.407	2	0.9898	0.9895	0.9887	0.9880	0.9869	0.9856	0.9836	0.9794	0.9898	0.9895	0.9887	0.988	0.9869	0.9856	0.9836	0.9794
7.407	2	0.9898	0.9895	0.9887	0.9880	0.9868	0.9856	0.9836	0.9794	0.9898	0.9895	0.9887	0.988	0.9868	0.9856	0.9836	0.9794
						difference from netlogo to excel ->				0	0	0	0	0	0	0	0

Fig. A.7 Memory decay output from model simulation in comparison to the same calculations performed in Excel. The difference of these values is 0, therefore, we can conclude that the memory decay was implemented correctly in the model.

						stone-cors of seals															
						1		2		3		4		5		6		7		8	
time	movement-mode c	xcor of seals	ycor of sea	target of seals	length st	xcor	ycor	xc	yc	xc	yc	xc	yc	xc	yc	xc	yc	xc	yc	xc	yc
7.391	3	69.47	60.88	**{patch 72 67}**	8	82	44	49	77	72	34	72	67	49	44	82	77	39	34	39	67
7.392	3	71.21	65.30	**{patch 72 67}**	8	82	44	49	77	72	34	72	67	49	44	82	77	39	34	39	67
7.392	FALSE	**72.00**	**67.00**	FALSE	8	**82**	**44**	49	77	72	34	**72**	**67**	49	44	82	77	39	34	39	67
7.394	FALSE	72.00	67.00	FALSE	8	**72**	**67**	**82**	**44**	49	77	72	34	49	44	82	77	39	34	39	67
7.395	FALSE	72.00	67.00	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.396	FALSE	72.00	67.00	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.398	1	72.00	67.00	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.398	1	70.33	64.28	{patch 65 56}	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.399	1	69.51	62.41	{patch 65 56}	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.399	1	67.54	58.87	{patch 65 56}	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.400	2	65.00	56.00	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.400	2	65.86	58.87	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.400	2	65.86	59.19	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.401	2	66.28	61.05	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.401	2	66.71	64.17	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.402	2	67.86	66.37	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.402	2	68.35	67.90	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.403	2	69.45	70.17	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.403	2	69.20	72.88	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.404	2	68.96	74.72	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.404	2	68.36	76.94	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.405	2	68.40	79.37	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.405	2	68.48	80.32	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.406	2	68.87	83.21	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.406	2	69.50	85.64	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.406	2	69.66	86.58	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.407	2	69.46	87.94	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67
7.407	2	68.91	90.11	FALSE	8	72	67	82	44	49	77	72	34	49	44	82	77	39	34	39	67

Fig. A.8 Output file from model simulation showing that once seal reaches predetermined haul out site (movement mode = FALSE), it is added to seal's memory (stone-cors of seals).

(7) Determination of target based on attraction values

Haul out site is chosen based on the attraction value, which is dependent on the distance from the seal and time, how recently seal has visited there. Attraction values were calculated also in Excel and compared to the values exported from the simulation (Distance / Memory value). The attraction values calculated in Excel matched the values obtained from NetLogo, therefore, we can conclude that the implementation is correct. The determination of the target was verified by comparing the position of the lowest value in the attraction list and the same position in stone-cors list (lists all visited haul out sites, the most recent visit first) to the target determined. The target was the same as given in stone-cors list resulting in lowest attraction value (shows the highest attraction as calculated by distance/memory).

(8) Swimming to target

After hauling out, seal selects a deep water patch from its memory and sets it as a target. Once the target is reached movement mode is switched from 1 to 2. Once seal gets exhausted movement mode 3 is switched. Seal selects a haulout site from its memory and sets it as a target and heads there. Output file written from simulation shows that the procedures describe above are implemented correctly (Fig. A.9).

time	movement-mode of seals	xcor of seals	ycor of seals	target of seals
7.368981481	2	93.1443318	29.8567418	FALSE
7.369444444	2	93.96724791	29.00554949	FALSE
7.369907407	3	94.04714543	28.94541309	FALSE
7.37037037	3	92.78263369	30.36627316	{patch 82 44}
7.370833333	3	90.97978942	31.99871506	{patch 82 44}
7.371296296	3	87.8658341	37.66177391	{patch 82 44}
7.371759259	3	84.40750946	40.48399208	{patch 82 44}
7.372222222	3	83.62430277	42.58991075	{patch 82 44}
7.372685185	FALSE	82	44	FALSE
7.374074074	FALSE	82	44	FALSE
7.375462963	FALSE	82	44	FALSE
7.376851852	FALSE	82	44	FALSE
7.378240741	FALSE	82	44	FALSE
7.37962963	1	82	44	FALSE
7.380092593	1	80.90132205	45.11433485	{patch 65 57}
7.380555556	1	80.30589017	46.02344615	{patch 65 57}
7.381018519	1	78.0060915	47.82970455	{patch 65 57}
7.381481481	1	75.52082855	49.42440548	{patch 65 57}
7.381944444	1	71.98862186	51.61071559	{patch 65 57}
7.382407407	1	71.38364267	52.14855272	{patch 65 57}
7.38287037	1	67.2939382	54.72738207	{patch 65 57}
7.383333333	1	67.49395267	54.947716	{patch 65 57}
7.383796296	1	66.96514293	55.66108739	{patch 65 57}
7.384259259	2	65	57	FALSE
7.384722222	2	66.37755993	54.67937335	FALSE
7.385185185	2	67.54375683	51.74796001	FALSE
7.385648148	2	68.02772335	49.18517448	FALSE
7.386111111	2	69.80748579	46.06416245	FALSE
7.386574074	2	70.84694181	44.81186589	FALSE
7.387037037	2	72.45581811	43.71411898	FALSE
7.3875	2	72.46354932	45.16182006	FALSE
7.387962963	2	71.92023515	47.23369088	FALSE

Fig. A.9 Output file written from model simulations showing that seal sets a target in movement modes 1 and 3, and moves to the determined target sites.

(9) Land avoidance direction

If there is land ahead in step length or smaller, seal calculates the amount of land on both sides and chooses the direction where there is less land. Implementation was tested by writing an output file from model run and importing it to Excel, where it was confirmed that the direction where there was less land was chosen by the seal (Fig. A.10).

time	[movement-mode]	[land-ahead]	[count-right]	[count-left]	[decision-right]	[decision-left]	[avoidance-mode-right]	[avoidance-mode-left]
7.395	[2]	[false]	[0]	[5]	[true]	[false]	[false]	[false]
7.396	[2]	[true]	[5]	[7]	[true]	[false]	[false]	[false]
7.396	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.397	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.397	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.398	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.398	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.399	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.399	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.400	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.400	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.400	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.401	[2]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.401	[3]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.402	[3]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.402	[3]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.403	[3]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.403	[3]	[false]	[5]	[7]	[true]	[false]	[false]	[false]
7.404	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.404	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.405	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.405	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.406	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.406	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.406	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.407	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.407	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.408	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]
7.408	[3]	[true]	[1]	[2]	[true]	[false]	[true]	[false]

Markup Area

Fig. A.10 Correct implementation on land avoidance was verified by importing the output file written from model simulation to excel.

6 Model output verification

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

Summary:

> **In the first phase, model was calibrated to data of one GPS/GSM tracked Saimaa ringed seal individual. After the calibration, the model was not able to reproduce patterns observed in independent datasets. Therefore, we re-calibrated one parameter on individual basis, and after this re-calibration, relatively good fit for the datasets was obtained.**

Model parameters are listed in Table A.2. Parameters *exhaustion-threshold* and moving-threshold are arbitrary, and thus, were not calibrated. Calibration for the rest of the parameters was performed in two phases. In the first phase, model was calibrated using pattern-oriented approach (Grimm and Railsback, 2012; Grimm et al., 2005) by finding the best fitting parameter set compared to a dataset from one adult Saimaa ringed seal individual (ER11). However, this calibration yielded poor fit for datasets used in validation. Therefore, in the second phase, *mean-speed-adults* parameter was separately calibrated for the five individuals used in model validation.

Table A.2 Model parameters and their meanings, values, units and sources for the parameter values. In addition, the procedures where the parameters are used are listed.

Parameter name	**Meaning**	**Value**	**Units**	**Procedure where used**	**Source**
exhaustion-threshold	Determines when to head to a haul out site	0.500	–	*Move*	Calibration
moving-threshold	Determines when to start moving after resting	0.100	–	*Rest* *Sleep-in-water*	Calibration

exhaustion-recovery-rate	The rate at which exhaustion decreases when resting	0.660	per 60 min	*Rest Sleep-in-water*	Calibration
ref-mem-decay-rate	Memory decay rate	0.210	per 60 min	*Decay-memory*	Calibration
exhaustion-rate-adults	Exhaustion rate	0.089	per 20 min	*Set-exhaustion-rates*	Calibration
mean-speed-adults	Mean speed value	100.000–350.000 depending on the individual used in parameterization	m/20 min	*Adjust-speed*	Calibration
sd-speed-adults	Standard deviation of speed	123.100	m/20 min	*Adjust-speed*	Calibration
mean-turning	Mean turning angle	0.109	degrees	*Adjust-turning-angle*	Calibration
sd-turning	Standard deviation of turning angle	15.680	degrees	*Adjust-turning-angle*	Calibration
land-distance	The distance how far seal can see when avoiding land	3.458	grid cells	*Avoid-land-decision*	Calibration
ho-distance	Maximum distance to haul out site, which initializes resting if seal is not exhausted	6.000	grid cells	*Move*	Calibration
ho-exhaustion-limit	Exhaustion must exceed the parameter value to initialize resting if seal is not exhausted	0.150	–	*Move*	Calibration

Individual ER11 was selected to be used in the parametrization because its tracking data had highest number of relocations within interval of 20 min (±5 min) among the datasets in University of Eastern Finland’s Saimaa ringed seal telemetry database. Furthermore, one of the objects was to test if the model was calibrated based on one individual, would it produce patterns observed in other individuals as well. The hypothesis behind this is that the variance in pattern *distance from home* is explained by the landscape, i.e. labyrinthine nature of Lake Saimaa. Therefore, by calibrating the parameters with one individual could in theory reproduce the patterns observed for the others.

Parameter estimation was performed in two rounds: first, parameters were varied over a large range; second, they were fine-tuned by being varied over a narrower range around the optimal values identified in the first round (Table A.3). In both cases, a Latin hypercube sampling design (Iványi et al., 1979) was used by means of the *tgp* R package (Gramacy, 2007; Gramacy and Taddy, 2010) to draw 800 parameter sets from the entire parameter space defined by the nine parameters selected for calibration. For each parameter set, the model was run ten times. Ten replicates was estimated to be sufficient based on our calculations of the coefficient of variance (CV, standard deviation divided by mean) for both patterns with 10 example parameter sets. When the variance started to stay stable, the number of repetitions was estimated to be sufficient. Based on the CVs for all example parameter combinations, 7 repetitions would be enough to capture the trends in this stochastic model. However, we used

10 repetitions per parameter set, to be on the safe side. To assess model performance, means of the output variables' medians were calculated and compared to telemetry data. Deviation from telemetry data was calculated according to:

$$Deviation = \frac{|Obs-Sim|}{Obs},$$

where *Obs* is the observed median for the two variables calculated from the telemetry data, while *Sim* is the mean of the model runs' medians of the given output variables.

Based on the first round of simulations and following a filtering approach (Wiegand et al., 2004), the parameter sets having deviation for the *moving duration* variable below 15% were selected; among the sets passing this first filter, only the parameter sets presenting a total combined deviation for both patterns below 500% were retained to determine the range for the second round of simulations. In this stage, the parameter set producing the lowest total deviation from telemetry data was chosen.

Table A.3 Ranges of parameter values used in parameter estimation.

Parameter	*Round 1*		*Round 2*	
	min	*max*	*min*	*max*
exhaustion-rate-adults	*0*	*1.00*	*0.05*	*0.09*
mean-speed-adults	*0*	*600.00*	*100.00*	*300.00*
sd-speed-adults	*0*	*200.00*	*100.00*	*200.00*
mean-turning	*-10.00*	*10.00*	*-5.00*	*5.00*
sd-turning	*0*	*180.00*	*10.00*	*60.00*
ref-mem-decay-rate	*0*	*1.00*	*0*	*0.35*
land-distance	*1.00*	*10.00*	*3.00*	*10.00*

Since the duration of haul out events is influenced only by one parameter, that is, exhaustion recovery rate, we calibrated this parameter alone via a sensitivity experiment (parameter range 0-1.00, steps 0.01). Exhaustion recovery rate was calibrated to allow seals to haul out for the time observed by Niemi et al. (2013a). Haul out does not include any stochastic elements among runs; therefore, one run per parameter value was performed. The variation within runs arises from the state of an individual entering haul out (i.e., exhaustion level). The parameter value producing the lowest deviation in comparison to telemetry data was chosen.

Simulations from the first model version did not yield a good fit to the patterns observed in the field for individual ER11 (Fig. A.11). All 10 replicates statistically differed (one-way ANOVA, $p < 0.05$) from the ER11 dataset in the case of the *distance from home* variable. Seals moved too far away from the initial site in the model runs in comparison to the ER11 dataset, i.e., the mean value for the distance from home variable was significantly higher (mean of ER11; 1.13 km, mean of the model replicates' means; 2.87 km, range 1.73—4.99 km). The model reproduced the *moving duration* pattern better, but only 2 out of 10 replicates did not significantly differ (one-way ANOVA, $p > 0.05$) from the field data. Seals moved too long between consecutive haul out events, i.e., the mean of the moving duration was significantly longer (mean of ER11; 13.89 h, mean of the model replicates' means; 16.38 h, range 15.55―18.88 h), and the model was not able to reproduce the short movements observed in the field (Fig. A.11).

Consequently, to add more reality in the movement behaviour, we tested an alternative structure to the first version of the *move* submodel in which haul out only occurred when the seal was exhausted and needed a rest (haul out submodel 1: haul-out-by-exhaustion) by implementing the assumption that haul out is possible when seals are exhausted or there is a suitable haul out site nearby (haul out submodel 2: haul-out-by-exhaustion-and-closeness). To do this, the parameters *ho-distance* and *exhaustion-ho-limit* (see Table A.2 for parameter description) were added and calibrated (*ho-distance;* values tested 0.1, 2.0, 4.0, 6.0, 8.0, 10.0; *exhaustion-ho-limit;* values tested 0.10, 0.15, 0.20, 0.25; 0.30) to determine the distance from which a seal can observe a haul out site and the minimum value of exhaustion at which haul out can be initialised to avoid a seal starting to haul out right after a previous haul out event. Parameters were calibrated to match the telemetry data of calibration individual ER11.

After these modifications, the tested patterns of calibration individual ER11 were better reproduced by the model. Regarding the *distance from home* variable, 2 out of 10 replicates did not statistically differ from the field data (mean of the model replicates' means; 2.15 km, range 0.90–5.20 km). Also, model fit was better for *moving duration* pattern, as 5 out of 10 replicates did not differ from the calibration dataset (mean of the model replicates' means; 11.68 h, range 9.11–15.33 h) (Fig. A.11).

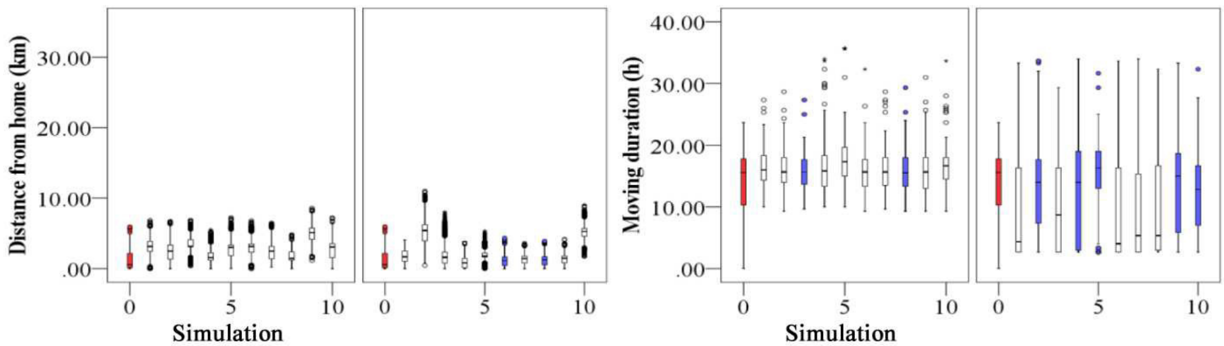

Fig. A.11 Distance from home (km) and moving duration (h) data of the Saimaa ringed seal individual (ER11) used for calibration compared to 10 simulation replicates (red box, i.e., 0 = observed data from seal individual, 1–10 = simulation replicates). For both output variables, box plots on the left were obtained using the first model version (haul out submodel 1: haul-out-by-exhaustion), and boxplots on the right where obtained after modifying model assumptions regarding haul out behaviour (haul out submodel 2: haul-out-by-exhaustion-and-closeness). Simulations with no statistical differences from observed data (one-way ANOVA, $p > 0.05$) are marked with blue colour. (○ = outliers 1.5 × inter quartile range (IQR) or more above the third quartile or 1.5 × IQR or more below the first quartile, ⋆ = outliers 3 × IQR or more above the third quartile or 3 × IQR below the first quartile)

After calibration of the optimal model structure, we tested the model performance on five independent datasets. Model failed to reproduce especially the *distance from home* pattern of the individuals used for validation. Depending on the individual in question, seals either moved too far or not far enough from the initial site in the model runs and/or had too long or too little time between consecutive haul out events compared to observed values. In the case of the *distance from home* pattern, there were statistically significant differences (one-way ANOVA, $p < 0.05$) in all replicates compared to field datasets. The *moving duration* pattern was well reproduced for individuals HE07 and KJ07 (the number of replicates that did not statistically differ were 9 and 8 out of 10, respectively); for the rest of the tested datasets, all replicates differed statistically from the observed values (Fig. A.12).

Since the global sensitivity analysis indicated that the *mean-speed-adults* parameter had the strongest effect on this model output, we calibrated this parameter separately for the five individuals used for model validation (tested ranges: ER11; 60–210 m/20 min, HE07; 250–400 m/20 min, KJ07; 250–400 m/20 min, OL10; 10–160 m/20 min, TO09; 110–300 m/20 min, VI09; 20–250 m/20 min). Simulations were replicated ten times. The parameter values resulting in the highest number of replicates that did not statistically differ from the observed datasets (one-way ANOVA, $p > 0.05$) were selected.

Re-calibrated mean speed values were: HE07-250 m/20min, KJ07-350 m/20min, OL10-100 m/20min, TO09-190 m/20min and VI09-100 m/20min. After re-calibrating this parameter, the fit for both output variables improved. Regarding the *distance from home* variable, all five tested individuals had a reasonably good fit. In the case of *moving duration* variable, the model reproduced patterns relatively well for three out of five tested datasets (Fig. A.12).

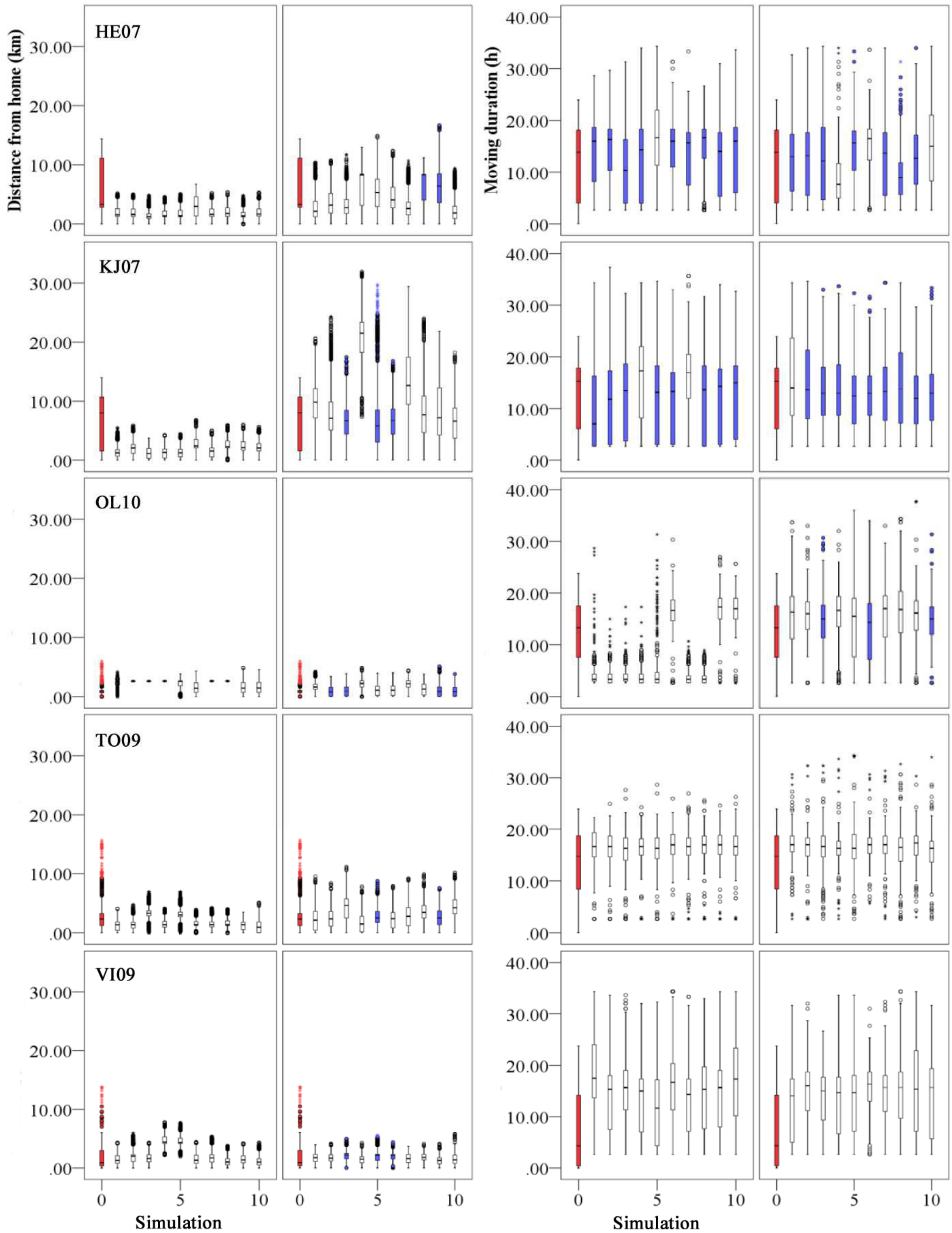

Fig. A.12 Distance from home (km) and moving duration (h) data of five GPS/GSM tracked Saimaa ringed seal individuals compared to 10 simulation replicates (0=observed data from seal individual, 1–10=simulation replicates). For both output variables, box plots on the left are based on calibration on one individual (ER11); boxplots on the right where obtained after recalibrating the mean speed parameter on an individual basis. Simulations with no statistical differences from observed data (one-way ANOVA, $p > 0.05$) are marked with blue colour. (○ = outliers 1.5 × inter quartile range (IQR) or more above the third quartile or 1.5 × IQR or more below the first quartile, ⋆ = outliers 3 × IQR or more above the third quartile or 3 × IQR below the first quartile)

The large variability in the mean swimming speed of adult seals cannot be captured with a single fixed value. We thus developed the probability distribution for the *mean-speed-adults* parameter based on re-calibration results and observed field data to account for such individual variability.

First, we analysed the swimming speeds recorded in the field for 18 GPS/GSM tracked individuals (Table A.3). One of the individuals (HE13) had multiple tracking seasons. The recorded dataset fitted a normal distribution with a mean value of 407.00 m/20 min and a standard deviation of 76.72 m/20 min. The parameter value for each newborn individual in the population model is drawn randomly from this normal distribution. This value is then multiplied by a scaling factor to match the resolution of the model parameter values. Such a scaling factor is drawn from a continuous uniform distribution ranging from 0.29 to 0.59 to introduce further individual variability. This range was calculated as follows: first, we calculated the ratio of the speed value obtained through calibration and the speed value observed in the field for each of the six individuals used to calibrate this parameter (Table A.4); then, we estimated the mean ratio across the six individuals (0.44) and added/subtracted 1.96 times the standard error of the mean.

Table A.3 Sex, open water tracking duration, number of locations and mean speed of the 18 GPS/GSM tracked individuals used for development of the probability distribution.

ID	Sex	Open water tracking duration (d)	Locations (n)	Mean speed (m/20 min)
JU07	M	218	4970	518.94
HE07	F	191	3003	367.15
VI09	M	199	5035	281.88
TO09	M	194	3092	505.44
OL10	F	180	1324	302.27
LI10	F	55	2000	340.55
ER11	M	125	3822	424.10
TE07	F	216	5192	313.90
AS12	M	196	5016	514.56
EE09	F	136	3103	378.47
VO12	M	188	1801	443.73
HE12	F	101	642	430.10
HE13 (1)	M	38	546	319.37
HE13 (2)	M	202	4085	407.92
SU97	F	102	1262	368.19
MI13	M	190	1838	397.35
LE14	M	181	2429	530.17
JE14	M	209	3589	426.71

NI14	M	204	2026	462.17

Table A.4 Observed and calibrated mean speeds and their ratio for six individuals used to calculate the scaling factor to match the observed speed distribution to model resolution.

ID	Observed mean speed m/20 min	Calibrated mean speed m/20 min	Observed/Calibrated ratio
KJ07	518.94	350	0.67
HE07	367.15	250	0.68
VI09	281.88	100	0.35
TO09	505.44	190	0.38
OL10	302.27	100	0.33
ER11	424.10	100	0.24

7 Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Summary:

Model outputs sensitivity to parameter values was tested. In addition, we analysed the effect of number and distribution of haul out sites on the simulated outputs.

We conducted a global sensitivity analysis to identify the model parameters with the strongest influence on model outputs, i.e., those that reduced the output variance most when fixed to their "true" values. We applied the variance-decomposition technique of Sobol (1993) to decompose the model outputs' variance into variances attributable to each input parameter while also evaluating the interaction between parameters. Sobol first-order sensitivity indices (S_i) measure the effect of varying a focus parameter alone but averaged over variations in other input parameters, thus providing information on the average reduction of output variance when the parameter is fixed. The total-effect indices (S_{Ti}) measure the contribution to the output variance of the focus parameter, including all variance caused by its interactions, of any order, with any other input parameters. We used the *sensitivity* R package (Pujol et al., 2016), which implements the Monte Carlo estimation of the Sobol's indices using the improved formulas of Jansen (1999) and Saltelli et al. (2010). The number of tested settings was given by $m \times (p + 2)$, where m is the size of the Monte Carlo sample matrix and p is the number of parameters to analyse.

We selected seven parameters that varied over the following ranges: Exh_{adult} (exhaustion-rate-adults; 0.01-0.25), sl_{adult} (mean-speed-adults; 10-600), $sl\text{SD}_{\text{adult}}$ (sd-speed-adults; 10-600), ta_{adult} (mean-turning; -10 - +10), $ta\text{SD}_{\text{adult}}$ (sd-turning; 10-100), M_{R} (ref-mem-decay-rate; 0-1), and *Vis* (land-distance; 1-10). We chose a sample matrix of size 400, and Sobol first-order and total-effect indices were computed for each parameter from a total number of runs of $400 \times (7 + 2) = 3600$.

The sensitivity analysis examined two model outputs: *moving duration* and *distance from home*. Because the location of haul out sites most likely influences the patterns, we simulated each of the parameter combinations keeping the same haul out site positions through all runs.

The simulations were performed for 4.066 months as long as the movements of the calibration individual were monitored in 2011. Model runs were replicated 2 times.

The global sensitivity analysis showed that variations in *moving duration* were driven only by the exhaustion rate of adults, while the mean swimming speed of adults had the strongest effects on the variable *distance from home*. Interactions between parameters were more important in the latter variable (Fig. A.13).

Fig. A.13 Results of sensitivity analyses conducted on the model's outputs; movement duration (a) and distance from home (b). ●= first-order indices ▲= total-effect indices

To study the effects of the number and location of haul out sites, we ran simulations initialising the model with 120, 240, 480, 960 and 1920 rocks. Haul out sites were either kept in the same locations between replicates or randomly distributed at the beginning of each replicate. In both scenarios, simulations were replicated five times at each haul out site density. Simulations were initialised from the same location where individual ER11 was captured in the field survey, and the model was run for 4.17 months. Furthermore, we examined the extent to which the stochastic initial selection of haul out sites and deep water areas during the warm-up period influenced model outputs. To do this, the seal was initialised having five fixed haul out sites and deep water patches in its memory; the obtained results were compared to simulations run using the normal settings, i.e., empty memory. Simulations were replicated 15 times, and the model was run for 4.17 months in each replicate.

The number of haul out sites had a significant effect on both output variables (full factorial two-way ANOVA, *distance from* home; $p < 0.001$, *moving duration*; $p < 0.001$) (Fig. A.14, A.15). The distribution of haul out sites (random distribution at the initialisation of each replicate or same locations in all replicates) had a significant effect on *distance from home* pattern ($p < 0.001$) (Fig. A.16). There was no effect on *moving duration* ($p = 0.104$) (Fig. A.17). Furthermore, the interaction between the number and distribution of haul out sites had significant effects on both patterns (*distance from* home; $p < 0.001$, *moving duration*; $p < 0.001$). In addition, the stochastic selection of haul out sites and deep water foraging areas during the warm-up period increases variability between replicates (Fig, A.18, A.19, A.20, A.21). The standard deviation of the mean was higher for both output variables if selection of haul out sites and deep water foraging areas were based on memory and distance factors (*distance from home*; 0.32 km, *moving duration*; 1.29 h) compared to if sites were predetermined (*distance from home*; 0.16 km, *moving duration*; 1.01 h). The coefficient of variation of *distance from home* and *moving duration was* 65.75% and 29.97%, respectively, when the sites were selected based on memory and distance factors, and 64.84% and 32.77%, respectively, when sites were predetermined.

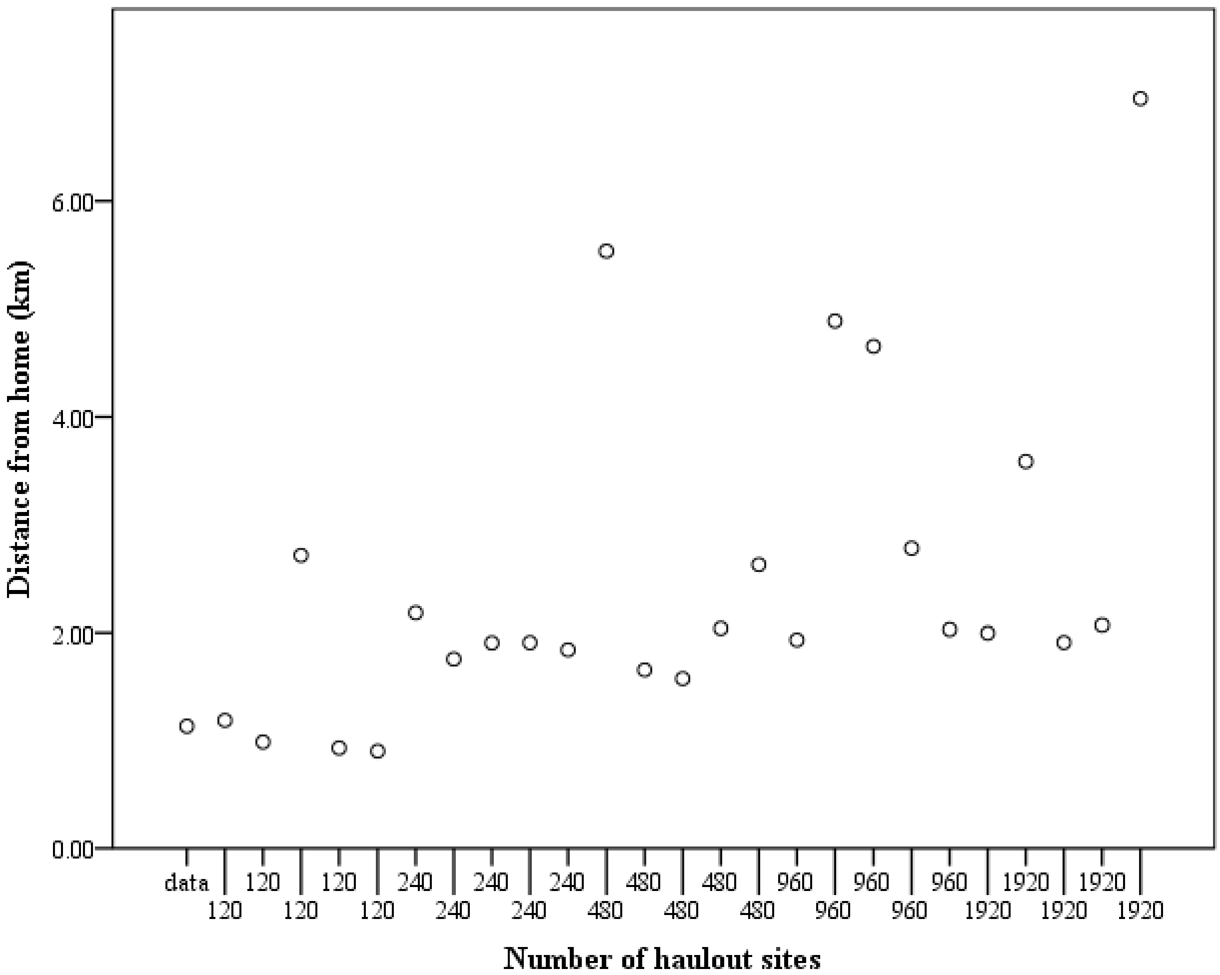

Fig. A.14 Mean of the distance from home variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Locations of haul out sites were kept constant at each density.

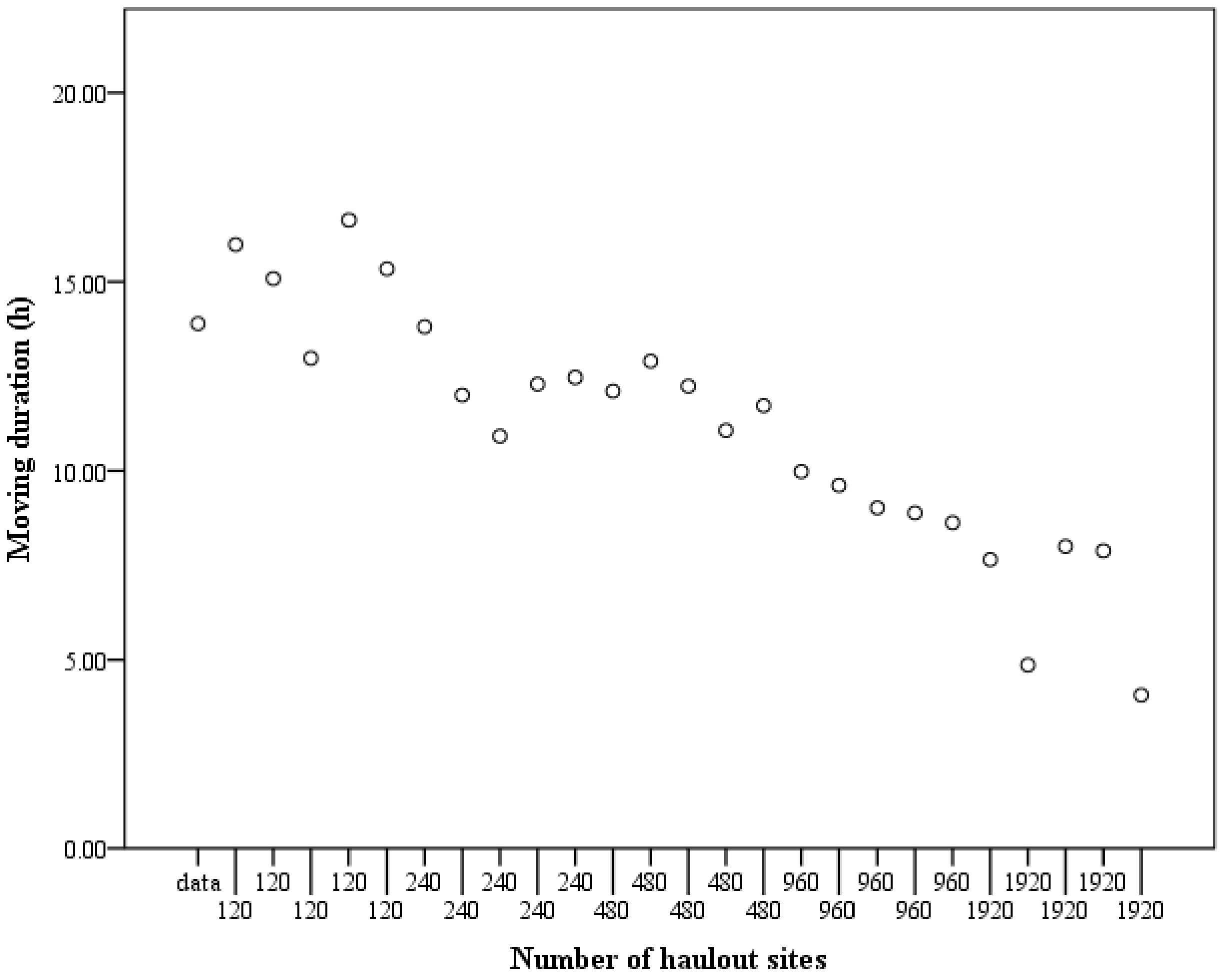

Fig. A.15 Mean of the moving duration variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Locations of haul out sites were kept constant at each density.

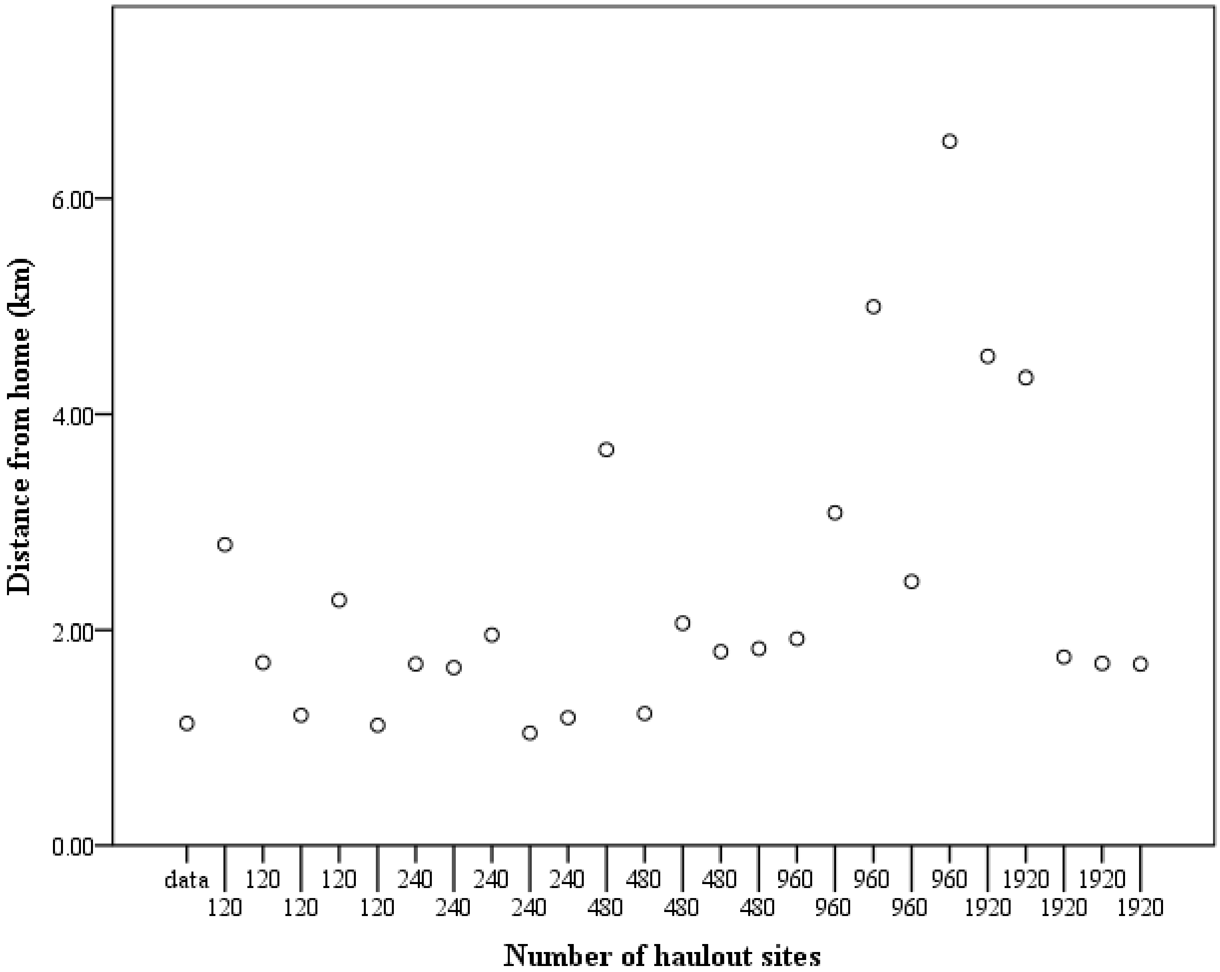

Fig. A.16 Mean of the distance from home variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Haul out sites were randomly distributed at the initialisation of each replicate.

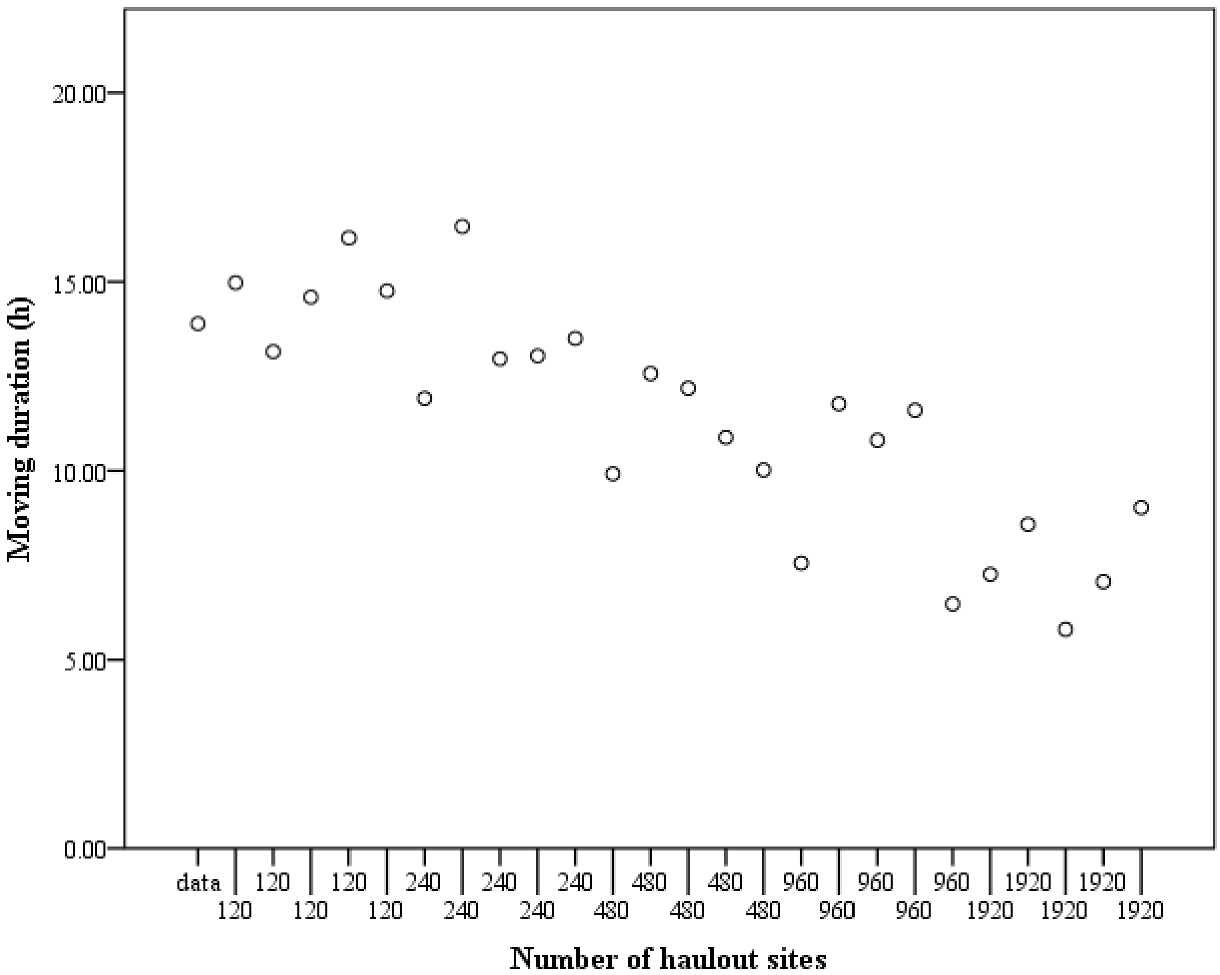

Fig. A.17 Mean of the moving duration variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Haul out sites were randomly distributed at the initialisation of each replicate.

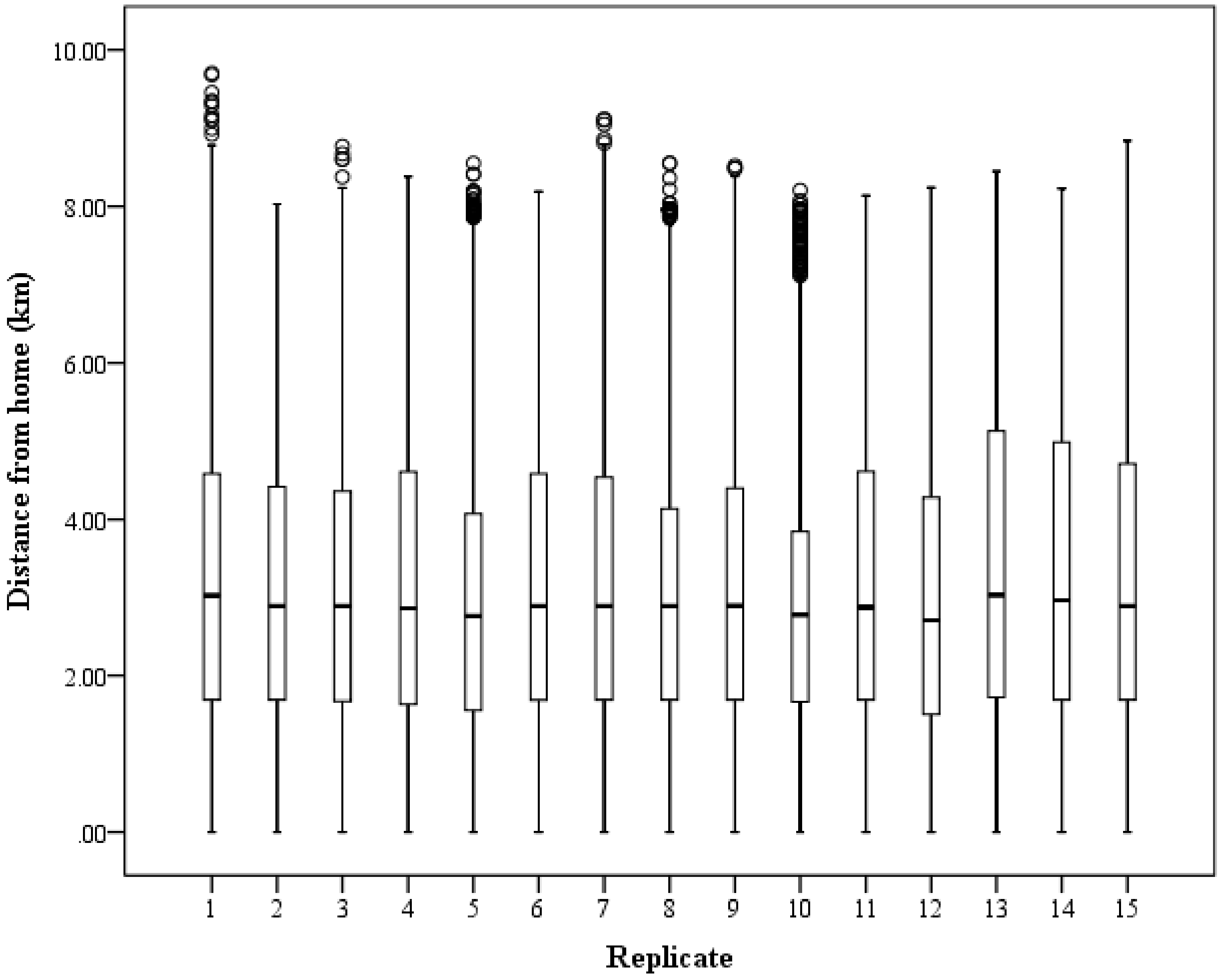

Fig. A.18 Distance from home (km) of 15 model replicates. Model was initialised with the seal having 5 haul out sites and deep water foraging areas in its memory; only these sites were used as targets for haul out and foraging.

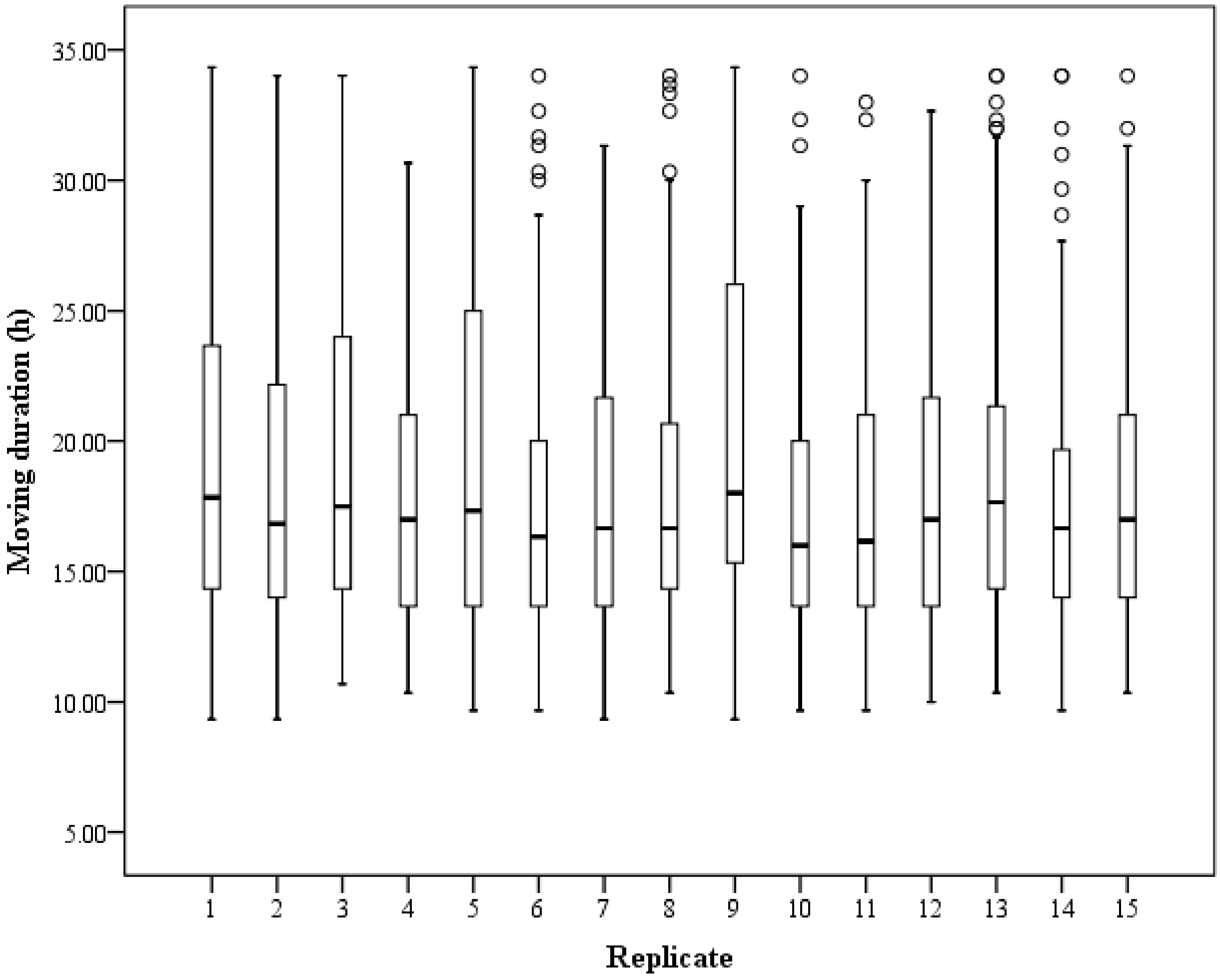

Fig. A.19 Moving duration (h) of 15 model replicates. Model was initialised with the seal having 5 set haul out sites and deep water foraging areas in its memory; only these sites were used as targets for haul out and foraging.

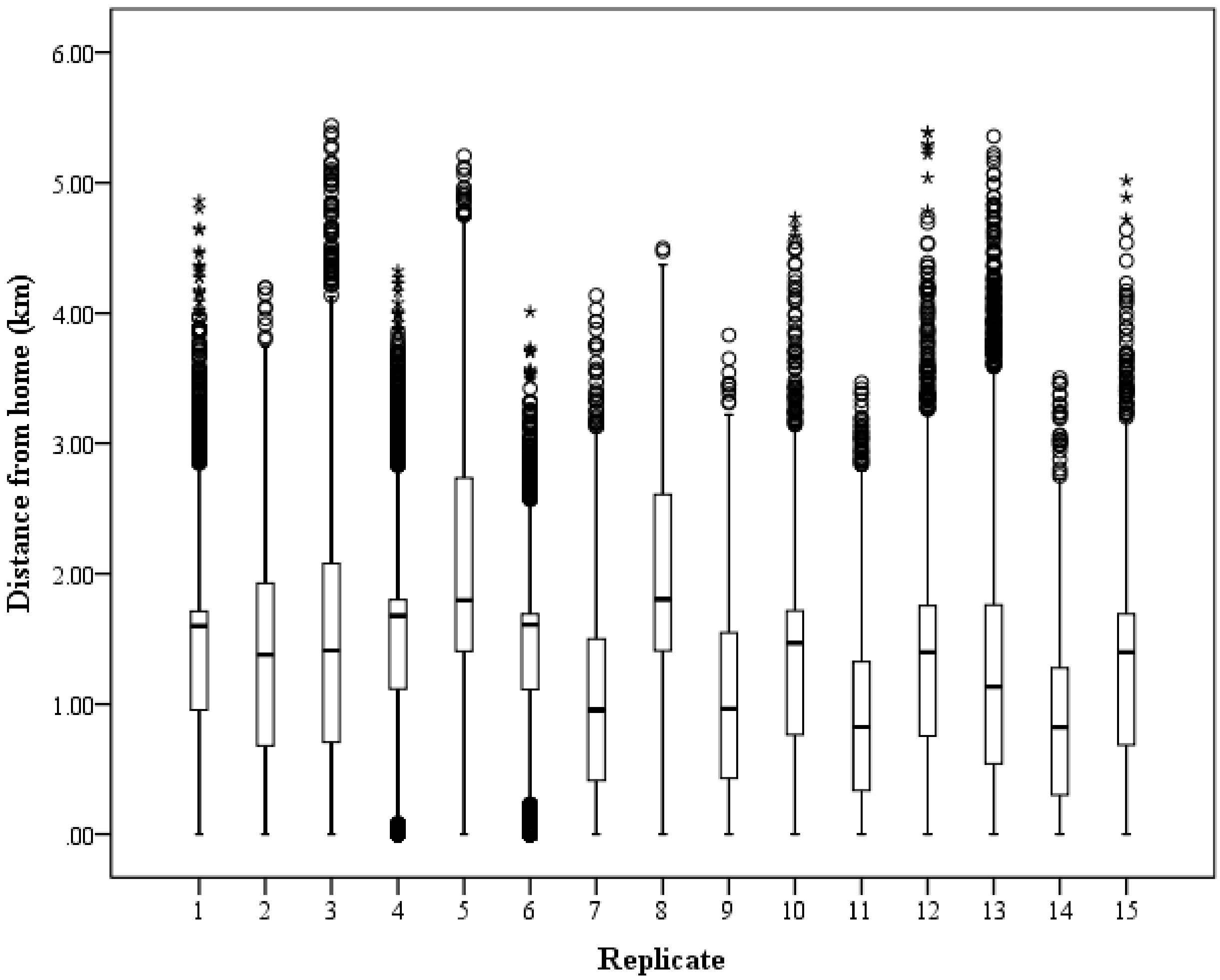

Fig. A.20 Distance from home (km) of 15 model replicates. Possibility to haul out on near-by haul out sites when the seal was not exhausted was disabled in these simulations, thus the selection was only based on distance and memory factors.

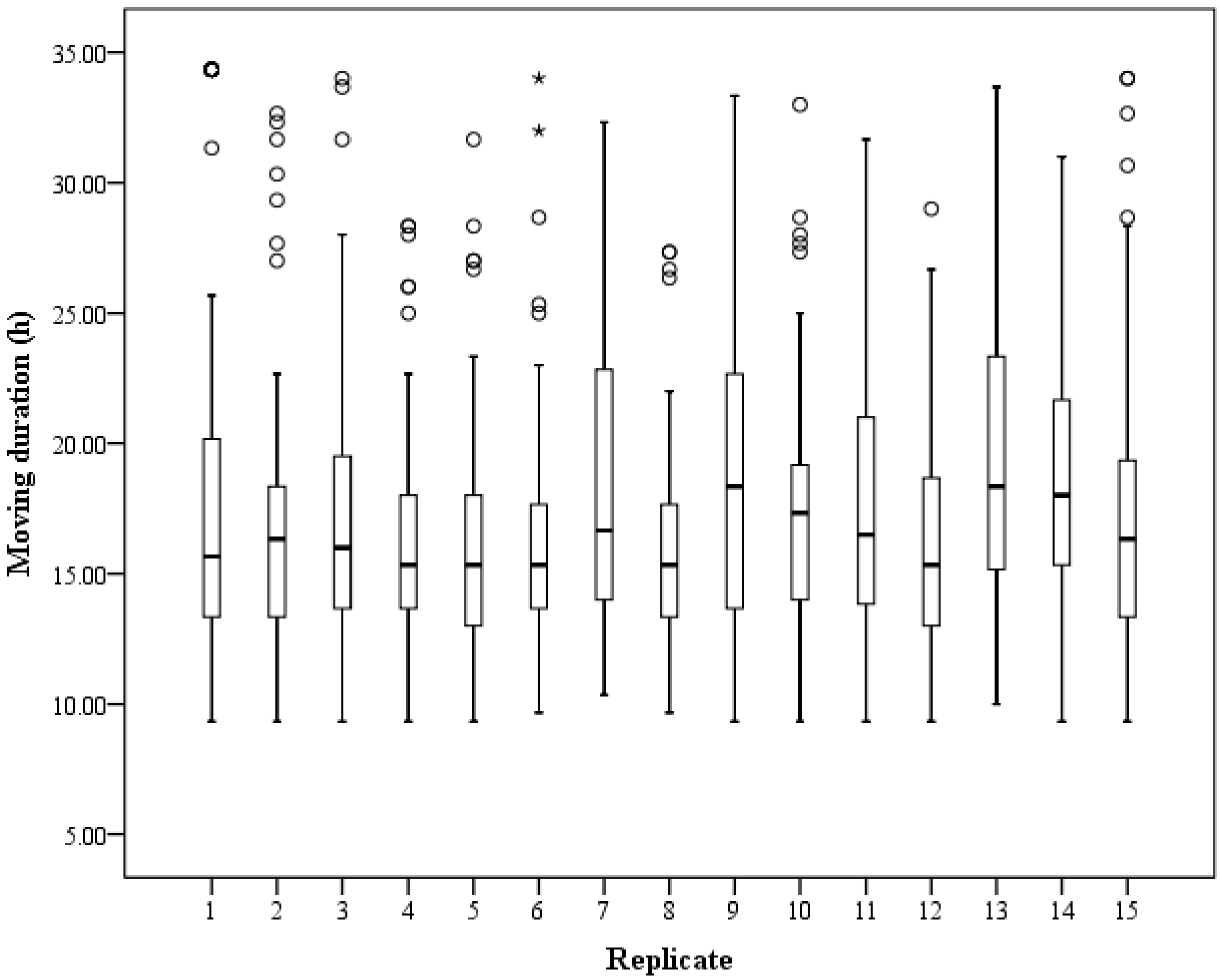

Fig. A.21 Moving duration (h) of 15 model replicates. Possibility to haul out on near-by haul out sites when the seal was not exhausted was disabled in these simulations, thus the selection was only based on distance and memory factors.

8 Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

Summary:

The model predictions were compared to independent data only after calibrating the model to dataset of ER11. However, the model failed to reproduce the patterns of independent datasets, and had to be re-calibrated using the datasets used for validation (see Chapter 6, Model output verification).

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Appendix B

Table B.1 Number of data points (n), mean, standard error (SE) of mean and standard deviation (SD) for distance from the home (km) variable of each individual. Each replicate (1–10) was compared to observed data (0), and deviation percentages were calculated using the equation: Deviation = (| Observed value – Simulated value |) / Observed value * 100. Column A's results are based on calibration on only individual ER11; column B's results were obtained after calibrating the mean speed parameter on an individual basis.

		A					B				
ID	**Replicate**	**n**	**Mean (km)**	**SE of mean**	**SD**	**Deviation (%)**	**n**	**Mean (km)**	**SE of mean**	**SD**	**Deviation (%)**
ER11	0	3829	1.13	0.02	1.21	0.00					
	1	3953	1.69	0.01	0.91	48.69					
	2	3949	5.06	0.03	1.87	346.71					
	3	3937	1.82	0.02	1.49	60.95					
	4	3859	0.90	0.01	0.80	20.29					
	5	3854	1.96	0.01	0.77	72.94					
	6	3874	1.07	0.01	0.73	5.61					
	7	3955	1.28	0.01	0.70	13.03					
	8	3955	1.17	0.01	0.78	3.65					
	9	3890	1.33	0.01	0.73	17.68					
	10	3920	5.20	0.02	1.08	358.70					
HE07	0	3003	6.60	0.08	4.41	0.00	3003	6.60	0.08	4.41	0.00
	1	5531	1.92	0.01	0.95	70.92	5602	2.62	0.03	2.00	60.35
	2	5557	1.91	0.01	0.94	71.08	5577	3.65	0.03	2.30	44.68
	3	5643	1.40	0.01	0.84	78.73	5612	3.09	0.03	2.01	53.19
	4	5607	1.67	0.01	0.83	74.70	5721	6.35	0.04	3.15	3.79
	5	5521	1.78	0.01	0.87	73.05	5466	5.44	0.04	2.75	17.62
	6	5542	3.00	0.02	1.62	54.48	5600	4.50	0.03	2.20	31.79
	7	5501	1.91	0.01	0.87	71.00	5578	2.76	0.03	1.87	58.16
	8	5561	2.01	0.01	0.93	69.59	5574	6.62	0.03	2.53	0.27
	9	5531	1.58	0.01	0.80	76.07	5585	6.55	0.05	3.47	0.80
	10	5620	1.93	0.01	0.93	70.80	5543	2.14	0.02	1.66	67.58
KJ07	0	4475	6.70	0.07	4.43	0.00	4475	6.70	0.07	4.43	0.00
	1	5655	1.24	0.01	0.83	81.46	5503	9.65	0.05	3.73	43.96
	2	5617	1.97	0.02	1.18	70.61	5491	7.88	0.06	4.49	17.55
	3	5700	1.21	0.01	0.96	82.01	5449	6.56	0.04	3.20	2.06
	4	5523	1.23	0.01	0.91	81.66	5485	21.11	0.06	4.18	214.87
	5	5591	1.26	0.01	0.88	81.22	5572	6.69	0.07	5.33	0.25
	6	5597	2.66	0.02	1.15	60.26	5568	6.66	0.05	3.39	0.69
	7	5528	1.40	0.01	0.97	79.06	5547	13.43	0.08	5.70	100.41
	8	5622	2.57	0.01	0.99	61.65	5564	8.10	0.06	4.37	20.86
	9	5552	2.34	0.02	1.16	65.07	5488	8.27	0.07	5.13	23.40
	10	5569	2.16	0.01	1.07	67.71	5565	6.40	0.05	3.59	4.49
OL10	0	2155	0.92	0.01	0.64	0.00	2155	0.92	0.01	0.64	0.00
	1	6156	2.50	0.01	0.50	171.03	5562	1.61	0.01	0.79	74.33

	2	6224	2.61	0.00	0.08	183.32	5590	0.93	0.01	0.85	0.47
	3	6238	2.61	0.00	0.09	183.12	5567	0.98	0.01	0.86	6.06
	4	6264	2.62	0.00	0.08	183.46	5596	2.12	0.01	0.67	130.26
	5	6071	2.18	0.01	0.81	136.08	5549	1.05	0.01	0.84	14.19
	6	5568	1.61	0.01	0.93	74.48	5547	1.08	0.01	0.87	16.72
	7	6410	2.62	0.00	0.08	183.68	5475	1.99	0.01	0.81	115.20
	8	6317	2.62	0.00	0.08	183.60	5505	1.28	0.01	1.01	39.15
	9	5511	1.64	0.01	0.94	78.20	5541	0.98	0.01	0.93	6.76
	10	5569	1.66	0.01	0.94	79.50	5577	0.94	0.01	0.84	2.16
TO09	0	3254	2.56	0.04	2.08	0.00	3254	2.56	0.04	2.08	0.00
	1	5524	1.23	0.01	0.90	51.91	5561	2.18	0.02	1.76	14.73
	2	5568	1.31	0.01	0.83	48.85	5510	2.37	0.02	1.64	7.39
	3	5592	3.27	0.01	1.07	27.63	5466	4.35	0.03	2.25	69.76
	4	5588	1.41	0.01	0.87	44.79	5534	1.66	0.02	1.49	35.10
	5	5561	3.04	0.02	1.27	18.85	5548	2.63	0.02	1.48	2.54
	6	5544	1.51	0.01	0.74	41.17	5600	2.23	0.02	1.59	12.76
	7	5475	1.38	0.01	0.81	46.11	5524	2.70	0.02	1.80	5.65
	8	5501	1.52	0.01	0.83	40.78	5585	3.39	0.02	1.39	32.49
	9	5526	1.23	0.01	0.83	51.79	5538	2.52	0.02	1.59	1.74
	10	5472	1.08	0.01	0.99	57.97	5599	4.49	0.02	1.62	75.46
VI09	0	4618	1.99	0.04	2.77	0.00	4618	1.99	0.04	2.77	0.00
	1	5483	1.37	0.01	0.78	31.25	5553	1.65	0.01	0.80	17.10
	2	5466	1.87	0.01	1.04	5.73	5562	1.63	0.01	0.70	17.85
	3	5545	1.60	0.01	0.78	19.74	5568	2.04	0.01	0.69	2.46
	4	5535	4.73	0.01	0.89	138.01	5572	1.41	0.01	0.74	28.99
	5	5689	4.56	0.01	0.83	129.49	5526	1.96	0.01	0.95	1.57
	6	5502	1.42	0.01	0.86	28.55	5588	1.93	0.01	0.58	2.77
	7	5588	1.82	0.02	1.15	8.37	5546	1.55	0.01	0.78	22.00
	8	5450	1.12	0.01	0.72	43.90	5585	1.78	0.01	0.64	10.55
	9	5602	1.40	0.01	0.72	29.63	5414	1.27	0.01	0.76	36.01
	10	5517	1.11	0.01	0.75	44.04	5574	1.42	0.01	0.87	28.59

Table B.2 Number of data points (n), mean, standard error (SE) of mean and standard deviation (SD) for the moving duration (h) variable of each individual. Each replicate (1–10) was compared to observed data (0), and deviation percentages were calculated using the equation: Deviation = (| Observed value – Simulated value |) / Observed value * 100. Column A's results are based on calibration on only individual ER11; column B's results were obtained after calibrating the mean speed parameter on an individual basis.

		A					**B**				
ID	**Replicate**	**n**	**Mean (h)**	**SE of mean**	**SD**	**Deviation (%)**	**n**	**Mean (h)**	**SE of mean**	**SD**	**Deviation (%)**
ER11	0	100	13.89	0.57	5.66	0.00					
	1	199	9.79	0.58	8.16	29.53					
	2	161	13.44	0.59	7.47	3.22					
	3	190	10.32	0.56	7.69	25.71					
	4	150	12.91	0.70	8.52	7.05					
	5	140	15.33	0.48	5.64	10.40					
	6	196	9.96	0.65	9.14	28.32					
	7	217	9.11	0.51	7.51	34.39					
	8	202	9.79	0.55	7.87	29.54					
	9	151	13.60	0.62	7.67	2.04					
	10	156	12.52	0.53	6.56	9.84					
HE07	0	126	11.93	0.67	7.48	0.00	126	11.93	0.67	7.48	0.00
	1	220	14.21	0.47	6.98	19.07	229	12.65	0.45	6.77	6.01
	2	222	14.08	0.45	6.65	17.99	220	12.83	0.49	7.33	7.49
	3	270	10.96	0.45	7.32	8.13	240	13.28	0.60	9.23	11.29
	4	222	13.15	0.52	7.73	10.21	339	9.03	0.29	5.40	24.28
	5	236	17.06	0.63	9.69	42.97	214	14.46	0.40	5.89	21.16
	6	218	14.34	0.44	6.46	20.22	202	15.17	0.40	5.69	27.14
	7	235	13.36	0.42	6.44	11.96	215	12.88	0.50	7.39	7.95
	8	218	14.29	0.44	6.51	19.77	316	9.59	0.29	5.20	19.65
	9	242	12.72	0.46	7.11	6.62	231	12.84	0.44	6.73	7.63
	10	229	13.72	0.47	7.11	14.99	241	15.90	0.63	9.80	33.24
KJ07	0	136	12.73	0.63	7.30	0.00	136	12.73	0.63	7.30	0.00
	1	320	10.79	0.51	9.06	15.25	199	16.58	0.73	10.28	30.29
	2	294	12.19	0.57	9.69	4.27	173	15.42	0.72	9.47	21.16
	3	234	12.38	0.52	8.02	2.74	138	13.66	0.56	6.59	7.35
	4	188	16.73	0.71	9.70	31.45	139	14.18	0.61	7.21	11.38
	5	258	12.22	0.53	8.56	4.02	216	12.40	0.45	6.56	2.58
	6	264	11.30	0.45	7.33	11.20	233	12.85	0.37	5.64	0.96
	7	192	16.69	0.66	9.08	31.10	210	14.09	0.58	8.35	10.72
	8	264	11.64	0.49	7.98	8.56	184	15.33	0.67	9.13	20.43
	9	259	12.02	0.46	7.36	5.57	201	12.33	0.45	6.32	3.15
	10	207	13.16	0.54	7.81	3.37	237	12.97	0.44	6.74	1.91
OL10	0	102	12.08	0.65	6.53	0.00	102	12.08	0.65	6.53	0.00
	1	905	4.00	0.08	2.27	66.87	200	15.14	0.51	7.16	25.37
	2	980	3.74	0.04	1.34	69.04	198	15.11	0.40	5.67	25.10
	3	978	3.74	0.04	1.40	69.01	206	14.00	0.44	6.34	15.88
	4	971	3.77	0.04	1.36	68.81	196	15.36	0.46	6.48	27.14

	5	696	4.68	0.15	3.87	61.22	214	15.15	0.61	8.86	25.39
	6	200	15.58	0.37	5.26	28.94	207	13.60	0.50	7.13	12.58
	7	1000	3.69	0.04	1.21	69.48	191	15.30	0.50	6.94	26.70
	8	1030	3.60	0.04	1.13	70.22	188	16.76	0.64	8.78	38.71
	9	190	16.36	0.35	4.87	35.42	216	16.35	0.55	8.05	35.37
	10	194	16.05	0.36	5.04	32.84	206	14.05	0.41	5.90	16.34
TO09	0	99	12.99	0.73	7.29	0.00	99	12.99	0.73	7.29	0.00
	1	192	16.16	0.30	4.23	24.42	184	16.88	0.30	4.02	30.00
	2	202	15.49	0.35	4.90	19.29	172	16.08	0.38	4.98	23.83
	3	206	14.96	0.38	5.41	15.21	182	16.34	0.38	5.11	25.84
	4	199	15.64	0.34	4.73	20.41	173	16.32	0.31	4.13	25.67
	5	201	15.51	0.34	4.78	19.46	199	17.19	0.47	6.67	32.36
	6	191	16.28	0.32	4.40	25.40	185	16.84	0.26	3.52	29.70
	7	196	15.94	0.32	4.43	22.72	185	16.81	0.32	4.37	29.44
	8	198	15.71	0.37	5.18	20.99	188	15.97	0.38	5.26	23.00
	9	191	16.28	0.32	4.40	25.36	182	16.72	0.29	3.85	28.72
	10	197	15.75	0.36	5.05	21.32	195	15.66	0.31	4.36	20.57
VI09	0	183	7.35	0.53	7.21	0.00	183	7.35	0.53	7.21	0.00
	1	174	18.71	0.74	9.78	154.46	209	12.52	0.50	7.20	70.30
	2	196	13.77	0.49	6.87	87.26	184	14.80	0.49	6.67	101.17
	3	184	15.01	0.50	6.78	104.03	226	13.32	0.40	5.97	81.17
	4	229	13.38	0.44	6.73	81.94	181	13.05	0.55	7.33	77.41
	5	264	11.52	0.47	7.59	56.66	220	13.02	0.44	6.50	77.05
	6	181	16.45	0.66	8.86	123.73	202	15.02	0.41	5.87	104.22
	7	204	13.41	0.49	7.02	82.34	169	14.19	0.51	6.61	92.93
	8	137	14.53	0.67	7.86	97.53	224	15.18	0.55	8.29	106.46
	9	197	15.25	0.64	8.95	107.36	163	16.01	0.81	10.29	117.63
	10	147	17.26	0.82	10.00	134.69	158	14.17	0.63	7.97	92.65

Appendix C

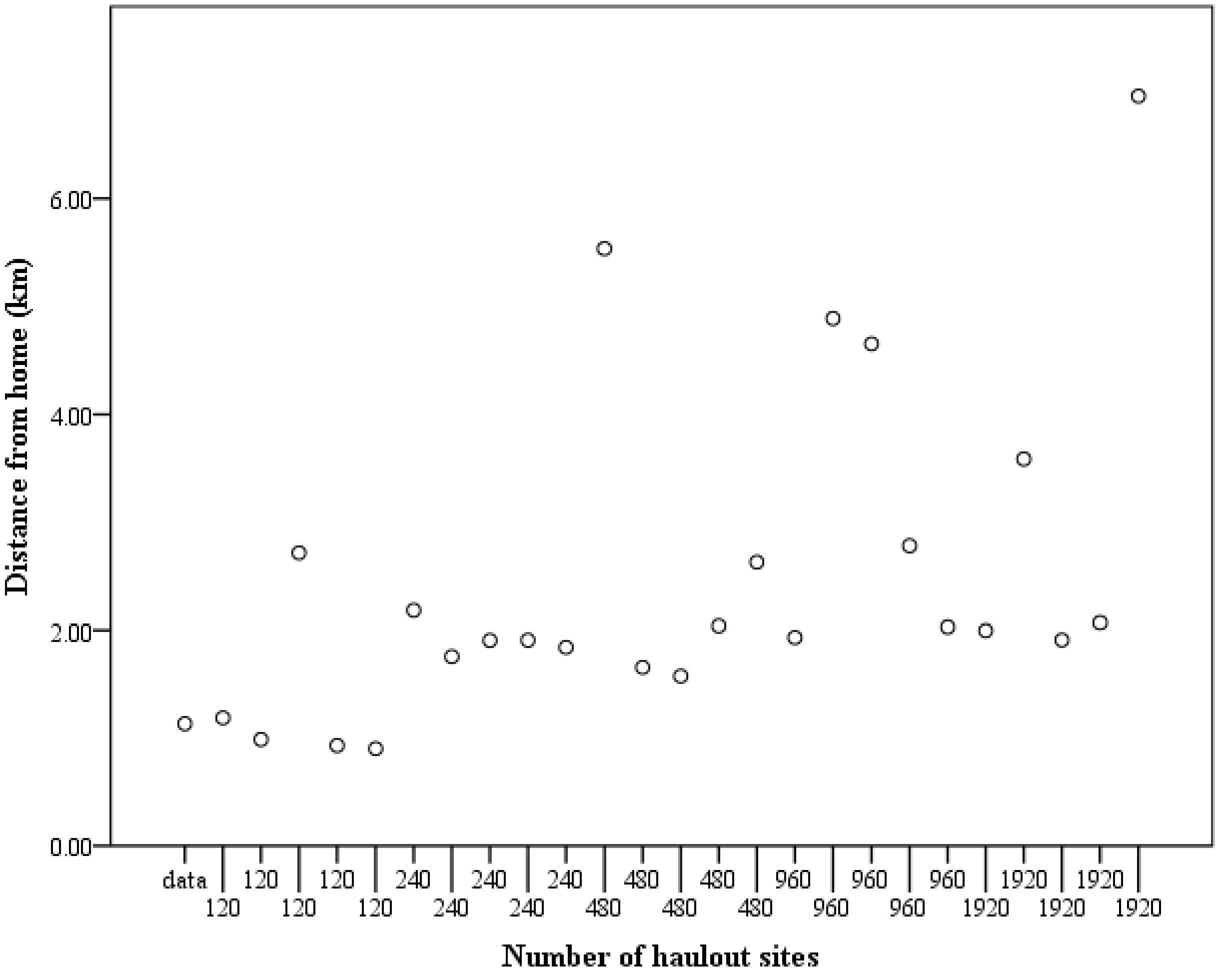

Fig. C.1 Mean of the distance from home variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Locations of haul out sites were kept constant at each density.

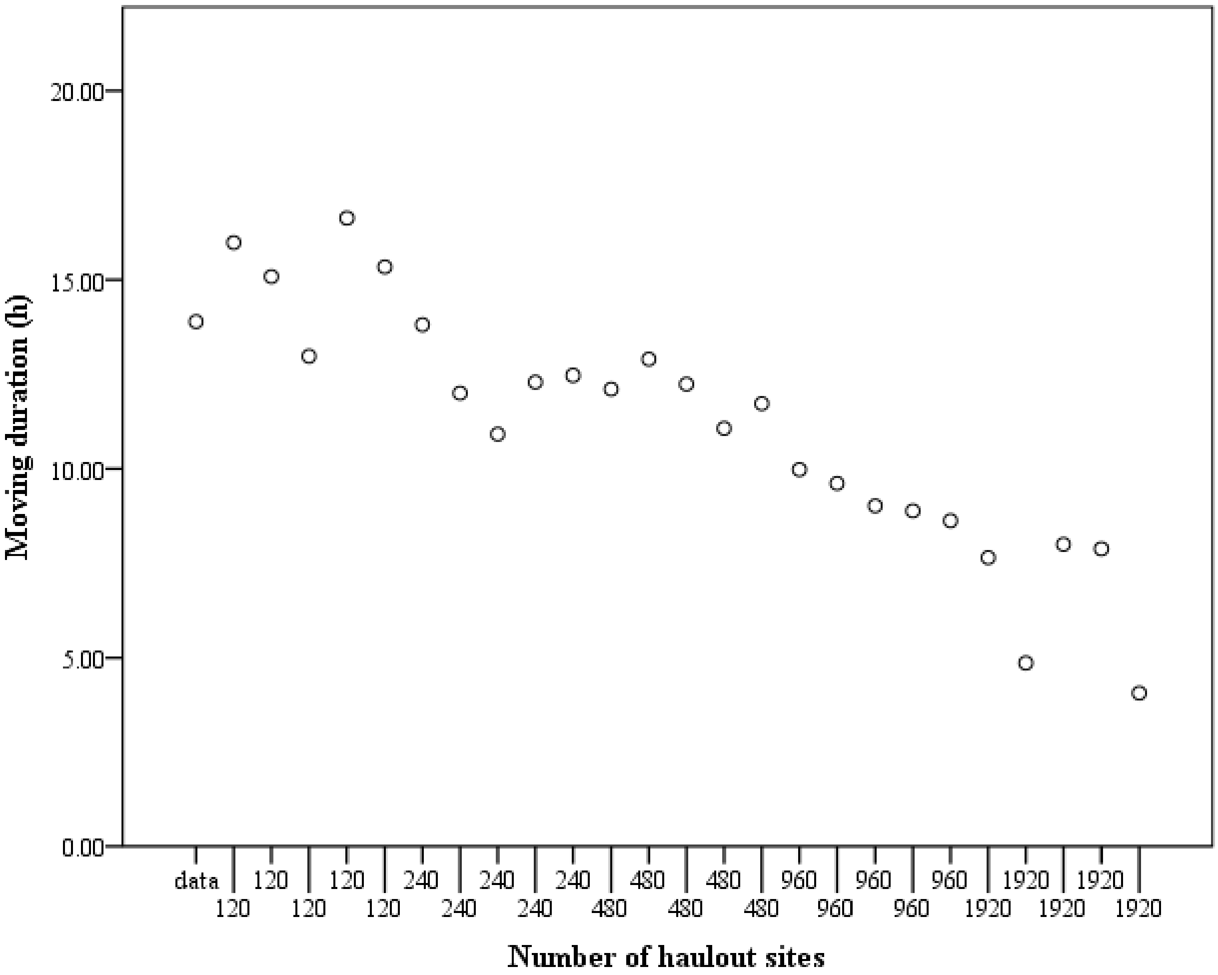

Fig. C.2 Mean of the moving duration variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Locations of haul out sites were kept constant at each density.

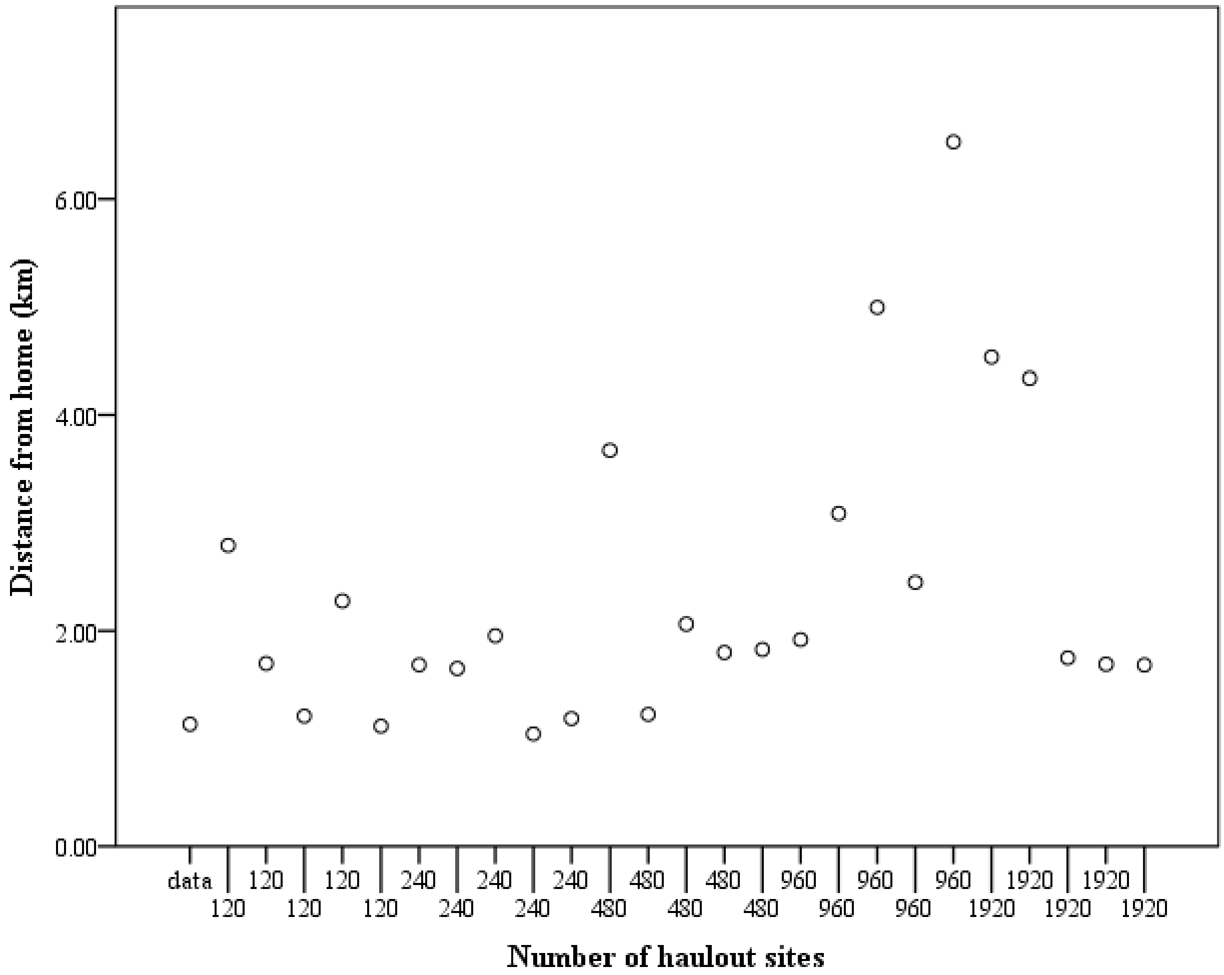

Fig. C.3 Mean of the distance from home variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Haul out sites were randomly distributed at the initialisation of each replicate.

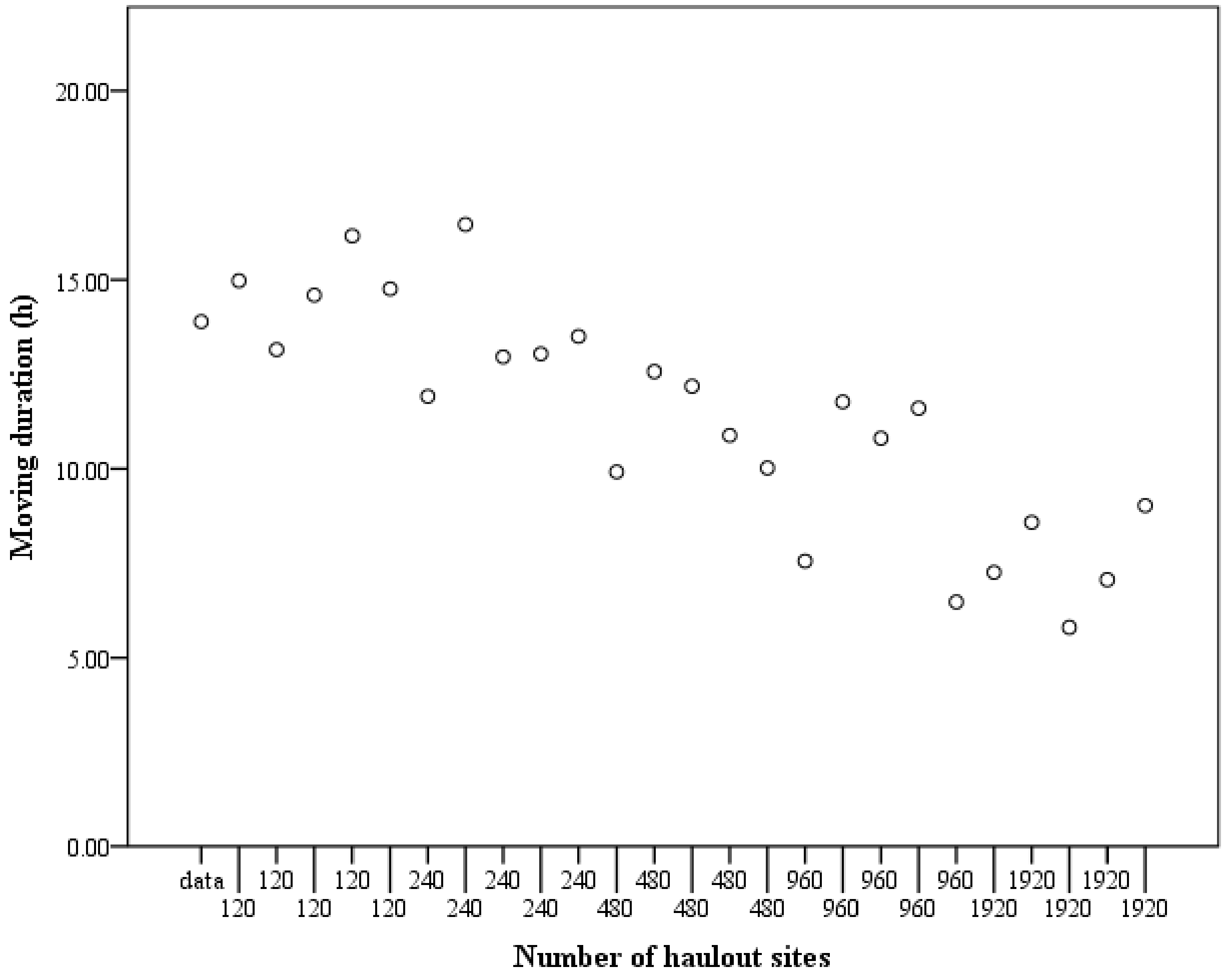

Fig. C.4 Mean of the moving duration variable on varying haul out site densities in model outputs and observed data of individual ER11 (data). Haul out sites were randomly distributed at the initialisation of each replicate.

Appendix D

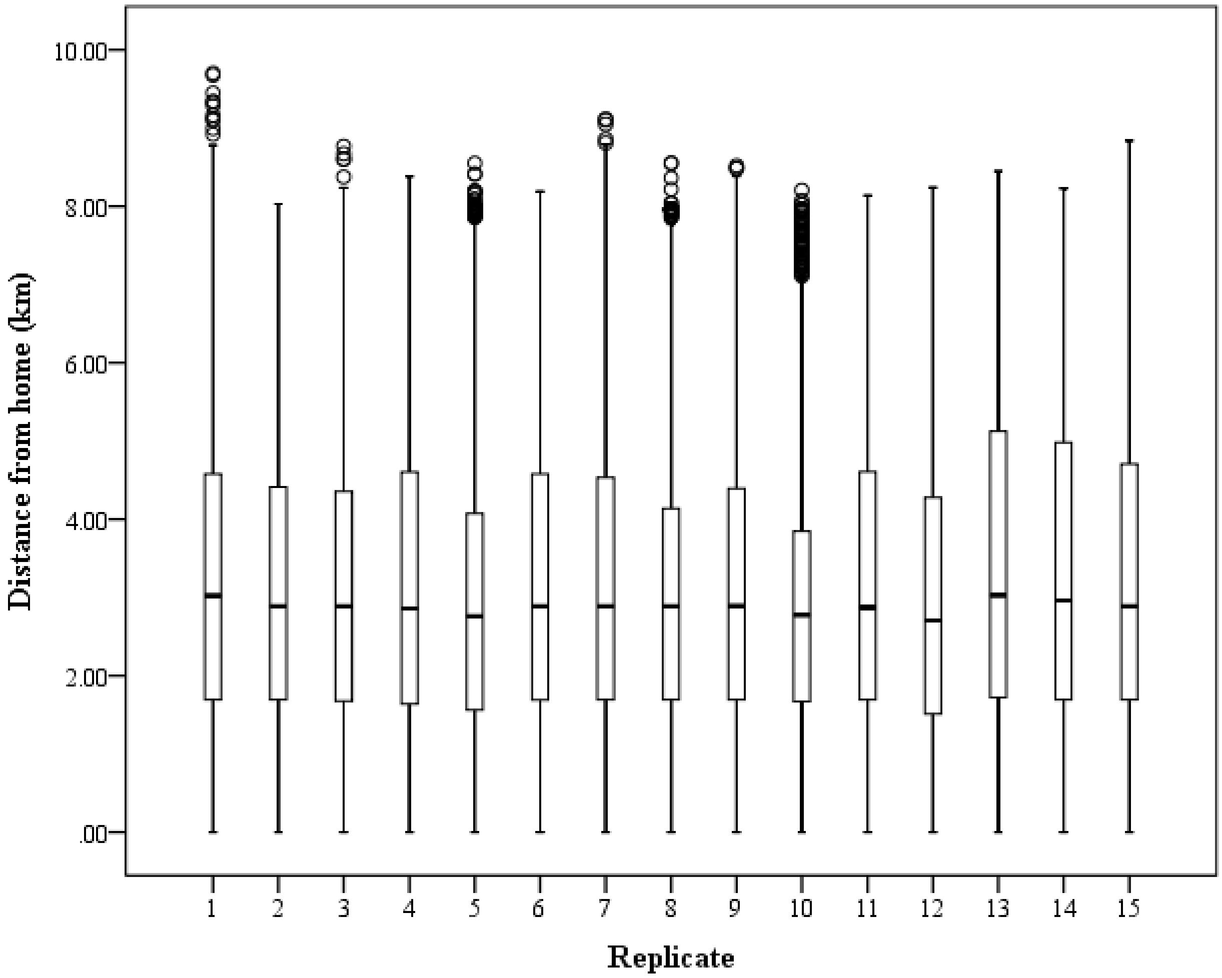

Fig. D.1 Distance from home (km) of 15 model replicates. Model was initialised with the seal having 5 haul out sites and deep water foraging areas in its memory; only these sites were used as targets for haul out and foraging.

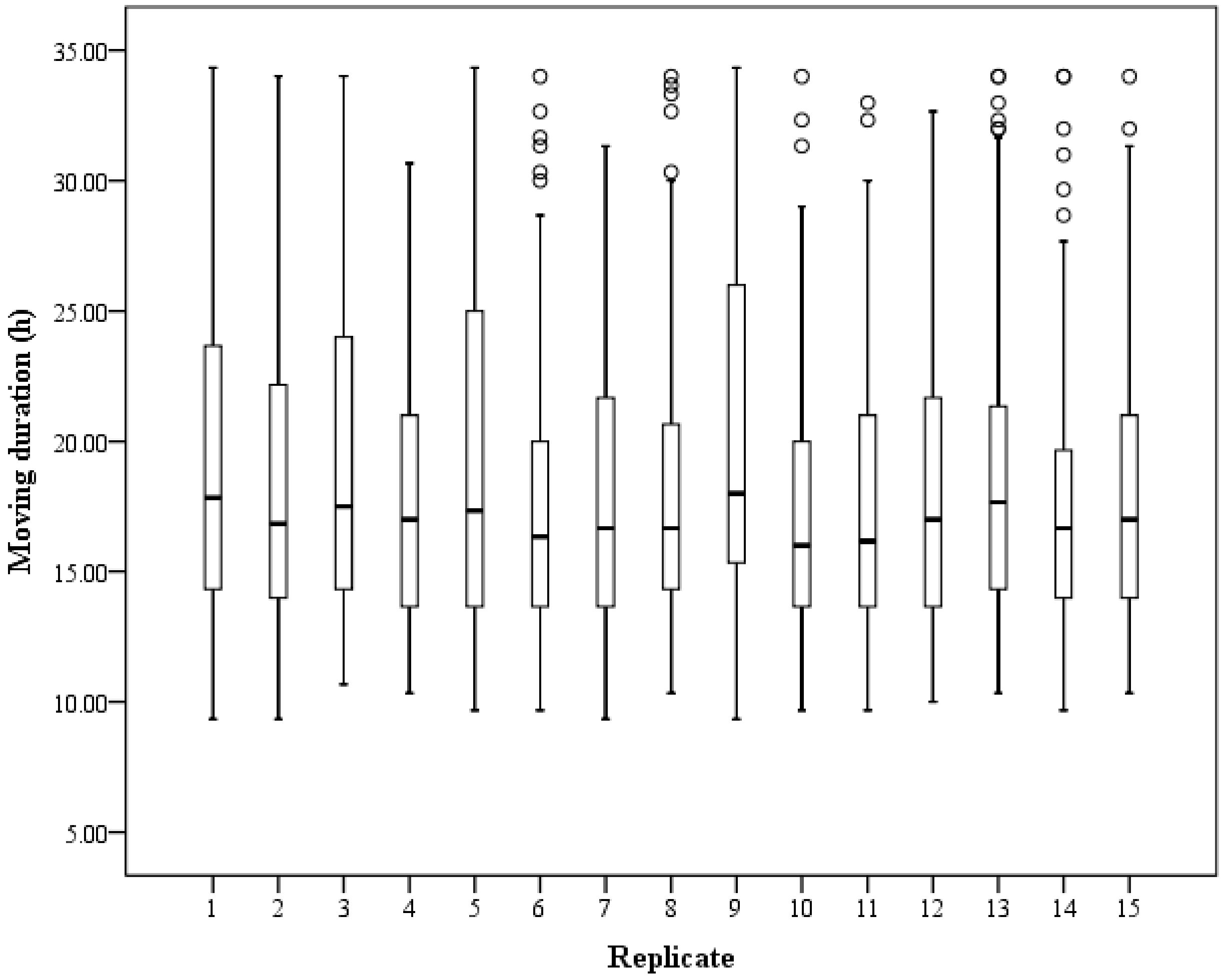

Fig. D.2 Moving duration (h) of 15 model replicates. Model was initialised with the seal having 5 set haul out sites and deep water foraging areas in its memory; only these sites were used as targets for haul out and foraging.

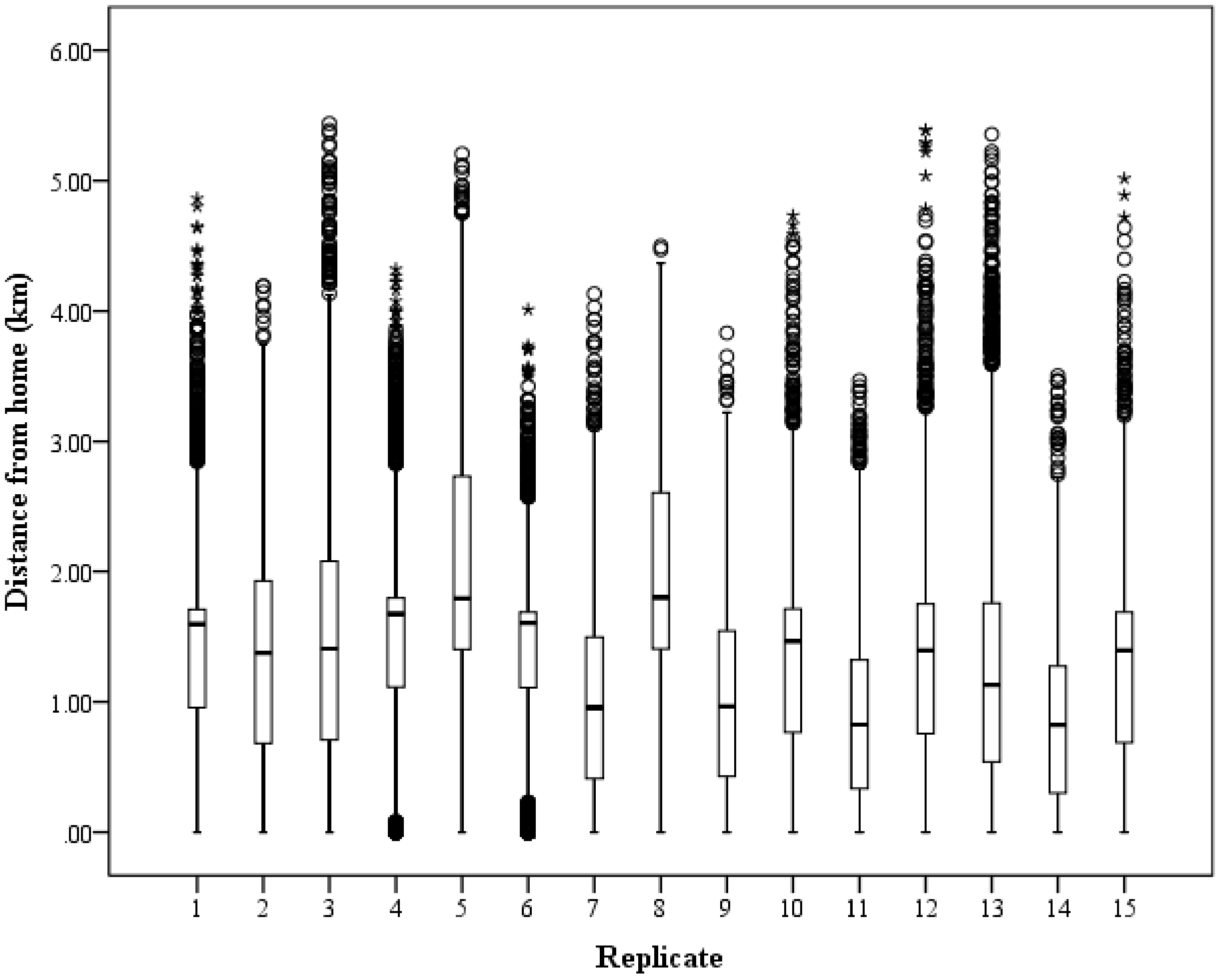

Fig. D.3 Distance from home (km) of 15 model replicates. Possibility to haul out on near-by haul out sites when the seal was not exhausted was disabled in these simulations, thus the selection was only based on distance and memory factors (see Materials and methods section for selection of haul out sites and foraging areas).

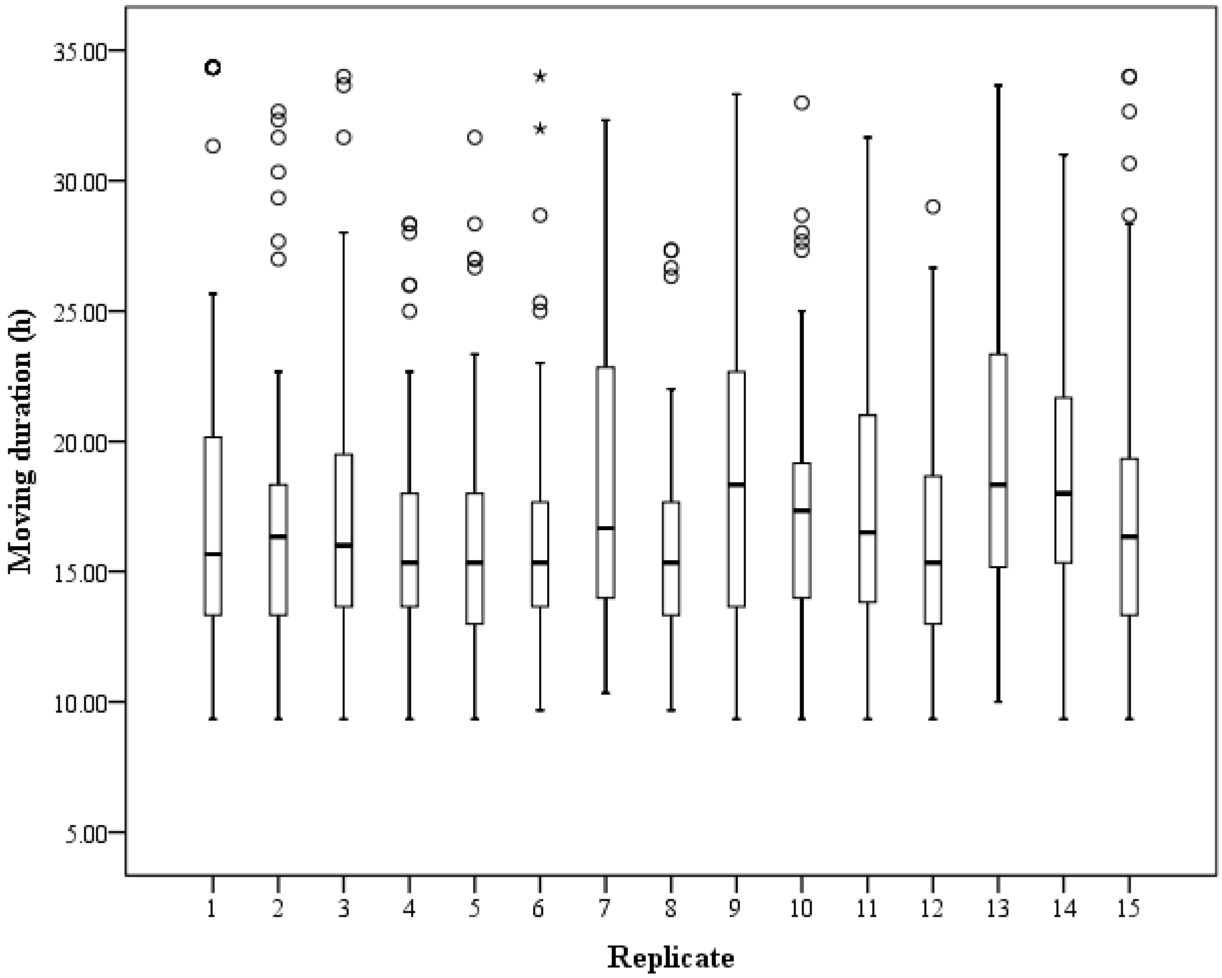

Fig. D.4 Moving duration (h) of 15 model replicates. Possibility to haul out on near-by haul out sites when the seal was not exhausted was disabled in these simulations, thus the selection was only based on distance and memory factors (see Materials and methods section for selection of haul out sites and foraging areas).

Appendix E

First, we analysed the swimming speeds for 18 GPS/GSM tracked individuals recorded in the Haukivesi, Joutenvesi and Pihlajavesi basins in 2007–2014 (see section *2.3 Telemetry data* for description of data collection) (Table E.1). One of the individuals (HE13) had multiple tracking seasons. The recorded dataset fitted a normal distribution with a mean value of 407.00 m/20 min and a standard deviation of 76.72 m/20 min. The parameter value for each new born individual in the population model would be drawn randomly from this normal distribution. This value is then multiplied by a scaling factor to match the resolution of the model parameter values. Such a scaling factor would be drawn from a continuous uniform distribution ranging from 0.29 to 0.59 to introduce further individual variability. This range was calculated as follows: first, we calculated the ratio of the speed value obtained through calibration and the speed value observed in the field for each of the six individuals used to calibrate this parameter (Table E.2) (see section *2.5. Model parameterization*); then, we estimated the mean ratio across the six individuals (0.44) and added/subtracted 1.96 times the standard error of the mean.

Table E.1 Sex, open water tracking duration, number of locations and mean speed of the 18 GPS/GSM tracked individuals used for development of the probability distribution.

ID	Sex	Open water tracking duration (d)	Locations (n)	Mean speed (m/20 min)
JU07	M	218	4970	518.94
HE07	F	191	3003	367.15
VI09	M	199	5035	281.88
TO09	M	194	3092	505.44
OL10	F	180	1324	302.27

LI10	F	55	2000	340.55
ER11	M	125	3822	424.10
TE07	F	216	5192	313.90
AS12	M	196	5016	514.56
EE09	F	136	3103	378.47
VO12	M	188	1801	443.73
HE12	F	101	642	430.10
HE13 (1)	M	38	546	319.37
HE13 (2)	M	202	4085	407.92
SU97	F	102	1262	368.19
MI13	M	190	1838	397.35
LE14	M	181	2429	530.17
JE14	M	209	3589	426.71
NI14	M	204	2026	462.17

Table E.2 Observed and calibrated mean speeds and their ratio for six individuals used to calculate the scaling factor to match the observed speed distribution to model resolution.

ID	Observed mean speed m/20 min	Calibrated mean speed m/20 min	Observed/Calibrated ratio
KJ07	518.94	350	0.67
HE07	367.15	250	0.68
VI09	281.88	100	0.35
TO09	505.44	190	0.38
OL10	302.27	100	0.33

ER11	424.10	100	0.24

```
extensions
[
  profiler
  gis
]

globals
[
 to-hours-scale
 resolution-scale
 time
 water-dataset
 islands-dataset
 deep-dataset
 run-number
 warm-up-counter
 age-counter
 ref-mem-decay-rate
 exhaustion-rate-adults
; mean-speed-adults
 sd-speed-adults
 mean-turning
 sd-turning
 land-distance
 number-of-rocks
]

breed [locations location]
breed [stones stone]
breed [seals seal]


patches-own
[
 land?
 stone-place?
 island?
 deep
]

stones-own
[init-site]

seals-own
[

;; For calculating home ranges
Name
X
Y
age-locations
```

```
my-patches
distances
a



;; Variables
age-in-months
exhaustion
exhaustion-rate ;; changes depending on age
target          ;; haul-out site (mode 3) or deep (mode 1)
head-current    ;; finding suitable turning angle
head-lt         ;; --
head-rt         ;; --
haul-out-dur    ;; only for reporting
haul-out-dur_report
moving-dur      ;; only for reporting
moving-dur_report     ;; reports moving dur just once, when initializing haul out
distance-from-home
step-taken      ;; reports the distance moved per time step
loc-prev        ;; reports the location in the previous time step
old-home        ;; birth site
count-left      ;; deciding the land avoidance direction
count-right     ;; deciding the land avoidance direction
turning-angle
step-lenght
mean-speed-adults

;; Parameters
;ref-mem-decay-rate
;exhaustion-rate-adults
;mean-speed-adults
;sd-speed-adults
;mean-turning
;sd-turning
;land-distance
exhaustion-threshold      ;;  when to start looking for haul-our site
moving-threshold          ;;  determines when to start moving again
exhaustion-recovery-rate
exhaustion-rate-newborns
mean-speed-pups
sd-speed-pups
age-maturity
age-dispersal
exhaustion-ho-limit
ho-distance

;; True/false -switches
sleep-water             ;; if exhaustion 0.999, keeps a seal sleeping in water
movement-mode           ;; 1, 2 or 3, false if hauling out
```

```
avoidance-mode-right      ;; if heading to target (modes 1 and 3) and an island ahead,
avoidance-mode-left       ;; keeps the land avoidance mode
right-finish              ;; finding a land avoidance mode
left-finish               ;; --
right-counter             ;; --
left-counter              ;; --
find-target               ;; in the beginning of modes 1 and 3, the seal defines a target patch
turning-counter

;; Lists
stone-cors                ;; stores haul-out locations
memory-stones-list        ;; decreases memory of the haul-out locations
deep-cors                 ;; stores last 100 deep water patches visited
is-land?                  ;; to avoid land
haul-out-age              ;; "age" of stone cors -- older than evaluation-season deleted to match with
data
haul-out-counter

;warm-up-counter
]

;-----------------------------------------------------------------------

to load-maps ;; NOTE: The map files must be separately downloaded to the desired directory.

 __clear-all-and-reset-ticks
set-patch-size 0.5
let minim 0
let maxim 1000
resize-world minim maxim minim maxim

;; resolution scale calculates one side of a patch [m]
;; 54498 is the lenght [m] of the world in reality
set resolution-scale (54498 / maxim)

; the coordinate system
gis:load-coordinate-system ("Hauki-Jouten_6/vesi_yli1ha_Hauki_multipart.prj")
; Load datasets
set water-dataset gis:load-dataset "Hauki-Jouten_6/vesi_yli1ha_Hauki_multipart.shp"
set deep-dataset gis:load-dataset "Hauki-Jouten_6/syvyys_yli15m_polygon_2.shp"
set islands-dataset gis:load-dataset "Hauki-Jouten_6/saaret_alle298ha.shp"

; Set the world envelope to the union of dataset's envelopes
gis:set-world-envelope
(gis:envelope-union-of
  (gis:envelope-of water-dataset)
  (gis:envelope-of deep-dataset)
  (gis:envelope-of islands-dataset)
 )

; Land
```

```
ask patches [
          set pcolor white
          set land? true
         ]

; Water
ask patches gis:intersecting water-dataset
         [
          set pcolor 99
          set land? false
         ]

; Deep water
ask patches gis:intersecting deep-dataset
         [
          set pcolor 98
          set land? false
          set deep true
         ]

; Islands
ask patches gis:intersecting islands-dataset
         [
          set pcolor 6
          set land? true
          ask neighbors [set stone-place? true]
         ]


; Prevents stone places to fall to land, water surrounded by land only or in deep water
ask patches
[
  if land? = true [set stone-place? false]
  if all? neighbors [land? = true] [set stone-place? false]
  if deep = true [set stone-place? false]
]

;; LAND AROUND THE WORLD, PREVENTS SEALS TO ENCOUNTER 'NOBODY'
ask patches with
([pxcor < minim + 17
or pycor < minim + 17
or pxcor > maxim - 17
or pycor > maxim - 17])
[set pcolor white
 set land? true]

;; initial site
create-stones 1
 [
   move-to patch-at init-x init-y; 595 555
   if stone-place? = FALSE
```

```
  [move-to one-of patches with [stone-place? = true] with-min [distance myself]]
  set init-site true
  set shape "circle"
  set color black
  ;set label "HOME_"
  ;set label-color red
 ]

;; HAUL OUT ROCKS
;; set rocks
 set number-of-rocks 120
 create-stones (number-of-rocks - 1)
  [
   set color black
   set shape "circle"
   set size 2
   move-to one-of stones with [init-site = true]
   loop
   [
    ifelse any? other stones-here
    [
     move-to one-of patches with [stone-place? = true]
    ]
    [
     stop
    ]
   ]
  ]

 set run-number 0

;; Get parameters
;file-open "LatinHypercube_parameters_pups.txt"
;
;if file-read = "exhaustion.rate.pups" [set exhaustion-rate-pups_list file-read]
;if file-read = "mean.speed.pups" [set mean-speed-pups_list file-read]
;if file-read = "sd.speed.pups" [set sd-speed-pups_list file-read]
;
;file-close


reset-ticks


end

;-----------------------------------------------------------------------------------------------

to setup

  reset-ticks
```

```
ask seals [die]
ask locations [die]
clear-all-plots
cd

;; SET DIRECTORY
set-current-directory directory-path

;; FOR WRITING RESULTS

ifelse reset-run-number
[
  set run-number 0
]
[
  set run-number run-number + 1
]


 let file-name-2 (word "Dist_home" ".csv")
 if (file-exists? file-name-2) [carefully [file-delete file-name-2] [print error-message]]
 file-open file-name-2
 file-print (word "date-and-time," date-and-time)
 file-print (word "number-of-rocks," number-of-rocks)
 file-print (word "warm-up," warm-up)
 file-print (word "run-time," run-time)
 file-print (word "init-x," init-x)
 file-print (word "init-y," init-y)
 file-print (word "same-rock-positions," same-rock-positions)
 file-print (word "skip-dispersal-phase," skip-dispersal-phase)
 file-print (word "evaluation-season," evaluation-season)
 file-print (word "directory-path," directory-path)
 file-print (word "reset-run-number," reset-run-number)
 file-print (word "behaviorspace-run-number," run-number)
 file-print "Dist_home"
 file-close

 let file-name-3 (word "Mov_dur" ".csv")
 if (file-exists? file-name-3) [carefully [file-delete file-name-3] [print error-message]]
 file-open file-name-3
 file-print (word "date-and-time," date-and-time)
 file-print (word "number-of-rocks," number-of-rocks)
 file-print (word "warm-up," warm-up)
 file-print (word "run-time," run-time)
 file-print (word "init-x," init-x)
 file-print (word "init-y," init-y)
 file-print (word "same-rock-positions," same-rock-positions)
 file-print (word "skip-dispersal-phase," skip-dispersal-phase)
 file-print (word "evaluation-season," evaluation-season)
 file-print (word "directory-path," directory-path)
 file-print (word "reset-run-number," reset-run-number)
```

```
  file-print (word "behaviorspace-run-number," run-number)
  file-print "Mov_dur"
  file-close




;; TIME SETTINGS
 set to-hours-scale 1

;; ROCKS
; if the same rock locations as in previous run is wanted, switch in interface
 ifelse (same-rock-positions)
 [
  ;; same location as before
  ask stones
  [set color black]

 ]
 [
  ;; new locations and rocks
  ask stones [die]
  ;; initial site
  create-stones 1
  [
  move-to patch-at init-x init-y
  if stone-place? = FALSE
  [move-to one-of patches with [stone-place? = true] with-min [distance myself]]
  set init-site true
  set shape "circle"
  set color black
  ;set label "HOME_"
  ;set label-color red
  ]
  create-stones (number-of-rocks - 1)
  [
   set color black
   set shape "circle"
   set size 2
   move-to one-of stones with [init-site = true]
   loop
   [
     ifelse any? other stones-here
     [
       move-to one-of patches with [stone-place? = true]
     ]
     [
       stop
     ]
   ]
  ]
```

```
 ]

 set warm-up-counter 0

; show number-of-rocks


;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;; SEALS
  ;; one seal created
  create-seals 1
  [
    ;; Calibrated ------------------------------------------------
    let scaling-factor random-float 0.30 + 0.29
    let observed-speed random-normal 407.00 76.72
    set mean-speed-adults scaling-factor * observed-speed

;    print mean-speed-adults

    set exhaustion-rate-adults 0.089
    set sd-speed-adults 123.1
    set mean-turning -0.109
    set sd-turning 15.68
    set ref-mem-decay-rate 0.210
    set land-distance 3.458

    set exhaustion-recovery-rate 0.660

    set exhaustion-rate-newborns 0.117
    set mean-speed-pups 37.31
    set sd-speed-pups 61.52

    set exhaustion-ho-limit 0.15
    set ho-distance 6.0

    ;-----------------------------------------------------------------
    set Name who
    set size 3
    set age-in-months 0
    set color blue
    move-to one-of stones with [init-site = true]
    set exhaustion 0.998
    set stone-cors []
    set stone-cors (list patch-here)
    set sleep-water false
    set memory-stones-list []
    set memory-stones-list fput 0.99 memory-stones-list
    set haul-out-age []
    set haul-out-age fput 0 haul-out-age
    set age-locations []
    set age-locations fput 0 age-locations
```

```
  set deep-cors []
  set target false
  set moving-threshold 0.100
;    set step-lenght 1
  set avoidance-mode-right false
  set avoidance-mode-left false
  set right-finish false
  set left-finish false
  set head-current false
  set head-rt false
  set head-lt false
  set right-counter 0
  set left-counter 0
  set is-land? []
  set haul-out-dur 0
  set haul-out-dur_report 0
  set moving-dur 0
  set moving-dur_report 0
  set old-home patch-here
  set movement-mode false
  set find-target false
  set age-maturity 48
  set age-dispersal 3
  set step-taken 0
  set distance-from-home 0
  set loc-prev patch-here
  ;; for calculating home ranges
  set X (list xcor)
  set Y (list ycor)
  set my-patches no-patches
  set distances []
  set a 0
  set haul-out-counter 0

  set warm-up-counter 0
  set age-counter 0
 ]
 set time 0

 ;;;;;;;;;;;;;;;;;;;; Validation Home range ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
 if write-coordinates
 [
   let output-file-name (word "Coordinates" ".csv")
   if (file-exists? output-file-name) [carefully [file-delete output-file-name] [print error-message]]
   file-open output-file-name
   file-type "X,"
   file-type "Y,"
   file-print "Seal"
   file-close
 ]
```

```
end

;---------------------------------------------------------------------------

to go

 ask seals
 [
  ;    profiler:start

  ;; UPDATE TIME
  ifelse movement-mode = false
  ;; an hour
  [set to-hours-scale 1]
  ;; 20 min; 20 min x 3 = 1h
  [set to-hours-scale 3]

  if skip-dispersal-phase = true and age-counter < 1
  [
   set age-in-months age-in-months + 48 ;3
   set age-counter 1
  ]


  ;; SET AGE, months
  set age-in-months age-in-months + (1 / to-hours-scale / 24 / 30)

  ; skip winter season (January-March) as we are looking at open water season
  ifelse skip-dispersal-phase = true
  [
  let age-in-months-temp age-in-months - 3
  if age-in-months-temp = floor 9 or remainder (floor age-in-months-temp - 9)(12) = 0
  [set age-in-months age-in-months + 3]
 ;  print word "Age: " precision age-in-months 1
  ]
  [
  if age-in-months = floor 9 or remainder (floor age-in-months - 9)(12) = 0
  [set age-in-months age-in-months + 3]
 ;  print word "Age: " precision age-in-months 1
  ]

  ifelse skip-dispersal-phase = true
  [set time age-in-months - 48 ;3]
  [set time age-in-months]

  list-coordinates

  ;; MOVEMENT
  ifelse skip-dispersal-phase
  [
```

```
      decay-memory
      remember-haul-outs
      rest
      move

    ]
    [
      ; seals start moving at the age of 1 month (if not only adult phase is simulated)
      if age-in-months > 1
      [
       decay-memory
       remember-haul-outs
       rest
       move

      ]
    ]



;; MARKS LOCATIONS AS IN THE DATA
;   hatch-locations 1
;   [
;     set shape "circle"
;     set size 2
;     set color blue
;   ]

;; DEBUGS
if land? = true
[show "in land!"
 move-to one-of patches with [land? = false] with-min [distance myself] ]


;; Write files
if time > warm-up + 0.5 ; After the warm-up period seal has its initials site as target for haul out for
0.5 months (2 weeks) before starting to write results.
 [
  write-results
 ]
]

  ; The model is allowed to "stabilize" before collecting results from the simulation.
  if time > warm-up and warm-up-counter < 1
  [
;    ask seals
;    [
;      set xcor init-x
;      set ycor init-y
;      set exhaustion 0.998
;      set movement-mode 2
```

```
;;      print "Hello world!"
;;      print movement-mode
;    ]
    clear-all-plots
    clear-drawing
    set warm-up-counter 1
  ]

  if time >= warm-up + 0.5 and warm-up-counter < 2
  [
    clear-all-plots
    clear-drawing
    set warm-up-counter 2
  ]


  report-distance-travelled
  plot-haul-out-duration
  plot-distance-from-home
  pen-down-illustration


;     profiler:stop

;      show word "exhaustion = " precision exhaustion 3
;      show word "movement-mode = " movement-mode
;      show word "target: " target
;
;      print profiler:report
;      profiler:reset
;      show "--------------TICK------------------"

  ;; TICKS

  if time > run-time
  [
    if write-coordinates
    [calc-homerange]
    ask seals [write-results]
    stop
  ]

;  export-all-plots (word "Testi" run-number ".csv")
  tick

end

;-----------------------------------------------------------------------
;; DECAY OF THE MEMORY, based on porpoise model by Nabe-Nielsen et al. 2013

to decay-memory
```

```
  if not empty? memory-stones-list
  [
    let memory-stones-list-temp []
    (foreach memory-stones-list
     [
      set memory-stones-list-temp lput (?1 - (ref-mem-decay-rate * (1 - ?1) * ?1) / to-hours-scale)
memory-stones-list-temp
     ]
    )
    set memory-stones-list memory-stones-list-temp

   ;; REMOVE ITEMS FROM MEMORY LIST, LAST ITEM IF THE MEMORY IS ALREADY LOW
   if last memory-stones-list < 0.00000001 or length memory-stones-list = 100
    [
     ask stones-on last stone-cors [set color black]
     set memory-stones-list remove (last memory-stones-list) memory-stones-list
     set stone-cors remove (last stone-cors) stone-cors
     if empty? memory-stones-list
     [let max-memory-stones 0.99
      set memory-stones-list fput max-memory-stones memory-stones-list
      set stone-cors fput old-home stone-cors
      ]
    ]
;  print length memory-stones-list
;  print memory-stones-list
;  print stone-cors
  ]
end

;;--------------------------------------------------------------------

to remember-haul-outs

if any? stones-here
 [
     ;;  DELETE MEMORY OF EARLIER VISIT TO THE SITE AND ADD MEMORY OF THE NEW VISIT
     if member? patch-here stone-cors
     [
       let remove-pos position patch-here stone-cors
       set memory-stones-list remove-item remove-pos memory-stones-list
       set stone-cors remove-item remove-pos stone-cors
       set haul-out-age remove-item remove-pos haul-out-age
     ]
     let max-memory-stones 0.99
     set memory-stones-list fput max-memory-stones memory-stones-list
     set stone-cors fput patch-here stone-cors
     set haul-out-age fput 0 haul-out-age
]

;; haul-out-age - to match counting the number of haul out sites to evaluation season
```

```
;; enable comparison between model and data

   ;; update "age" of haul-outs
   let haul-out-age-temp []
   (foreach haul-out-age
     [
       ;; in every tick the age of the haul out increases, age given as months
       set haul-out-age-temp lput (? + ((1 / to-hours-scale / 24 / 30))) haul-out-age-temp
     ]
    )
   set haul-out-age haul-out-age-temp

   ;; delete older haul-outs from the count than the evaluation season
   ;; but without deleting the haul out locations from the stone-cors list
   ;; to enable seals to remember the site longer than the evaluation season
   set haul-out-counter haul-out-age
   foreach haul-out-counter
   [
     if ? > evaluation-season
     [set haul-out-counter remove ? haul-out-counter]
   ]
   ;; length of the counter gives the number of the sites during evaluation season

end

;;-------------------------------------------------------------------

;; HAUL OUT

to rest


  ;;THE SEALS ARE RESTING UNTIL THE EXHAUSTION DECREASES ENOUGH
  if movement-mode = false and sleep-water = false
  [
   set moving-dur 0
   set moving-dur_report 0
   ask stones-here [set color red]
   ;; scales the time step (hours)
   set haul-out-dur haul-out-dur + 1 / to-hours-scale
   ;; prevents exhaustion go above 1
   if exhaustion > 0.9999 [set exhaustion 0.9999]
   set exhaustion exhaustion - (exhaustion-recovery-rate * exhaustion * (1 - (exhaustion / 1)) / to-
hours-scale)

   if exhaustion < moving-threshold
   [
     set haul-out-dur_report haul-out-dur
;      ask seals [write-results]
     set haul-out-dur 0
     set find-target true
```

```
      set exhaustion 0.1
      ;; this is to prevent the decrease of exhaustion really low

      if time > warm-up + 0.5
      [
        ask seals [write-results]
      ]

      ifelse empty? deep-cors
      [
        set movement-mode 2
        ;; if the seal did not visit a deep site yet: random movements
      ]
      [
        set movement-mode 1
        ;; finds a deep site after haul out
      ]
    ]
  ]

end

;------------------------------------------------------------------
to move


;; INITIALIZE RESTING--------------------------------------------

;  ;; if not exhausted but haul out site near-by, go there
  if movement-mode = 1 or movement-mode = 2  and exhaustion > exhaustion-ho-limit
  [
    if (distance one-of stones with-min [distance myself] <= ho-distance)
    [
      see-if-land-ahead
      if empty? is-land?
      [
        set target min-one-of stones [distance myself]
        set step-lenght distance target
        set heading towards target
        fd step-lenght
        set movement-mode false
        set avoidance-mode-left false
        set avoidance-mode-right false
        set target false
;        print "Haul out"
;        print exhaustion
        if any? stones-here
        [set moving-dur_report moving-dur]
      ]
    ]
  ]
```

```
;print target

  ;; go to haul out if exhausted and there is a rock close (neighboring grids)
  if movement-mode = 3
  ;; assumption that haul outs are possible only when exhausted
  [
   if (distance one-of stones with-min [distance myself] <= step-lenght )
   [
     ifelse patch-here = target
     [
   ;    if patch-here = old-home and time >= warm-up and time <= warm-up + 0.5 [print "I'm at
home!"]
      set movement-mode false
      set avoidance-mode-left false
      set avoidance-mode-right false
      set target false
;       print "Haul out as usual"
      if any? stones-here
      [set moving-dur_report moving-dur]
     ]
     [
      see-if-land-ahead
      if empty? is-land?
      [
        set target min-one-of stones [distance myself]
        set step-lenght distance target
        set heading towards target
        fd step-lenght
        set movement-mode false
        set avoidance-mode-left false
        set avoidance-mode-right false
        set target false
;        print "Haul out as usual"
    ;     if patch-here = old-home and time >= warm-up and time <= warm-up + 0.5 [print "I'm at
home!"]
        if any? stones-here
        [set moving-dur_report moving-dur]
      ]
     ]
   ]
  ]

;; SLEEP IN WATER IF EXHAUSTION GOES TOO HIGH --------------------
;if sleep-water-possible
;[
 if deep != true
 [
   if exhaustion >= 0.999 or sleep-water = true
   [sleep-in-water
   ]
```

```
 ]
;]

;; MOVING --------------------------------------------------------
 if movement-mode != false
 [
   adjust-speed
   adjust-turning-angle
   set-exhaustion-rates
   remember-deep
   set haul-out-dur_report 0

   ; Increase exhaustion
   set exhaustion-threshold 0.5
   set exhaustion exhaustion + ((exhaustion-rate * exhaustion * (1 - (exhaustion / 1))))
   if exhaustion > 0.999 [set exhaustion 0.999]

   ;; LOOKING FOR FORAGING AREAS
   if movement-mode = 1
   [
     targeted-moving
   ]

   ;; RANDOM
   if movement-mode = 2
   [
     non-targeted-moving
   ]

   ;; LOOKING FOR HAUL OUT SITE
   if movement-mode = 3
   [
     targeted-moving
   ]

   ;; SWITCH TO MODE 3
   if movement-mode = 1 or movement-mode = 2
   [
     if (exhaustion > exhaustion-threshold)
     [
       set movement-mode 3
       set find-target true
     ]
   ]

   set moving-dur moving-dur + 1 / to-hours-scale
   ;; which is 3 for movement modes 1-3

 ]

end
```

```
;---------------------------------------------------------------------
to adjust-speed

  ;; JUVENILES AND ADULTS

    set step-lenght random-normal (mean-speed-adults / resolution-scale) (sd-speed-adults /
resolution-scale)
 ;   print word "Step length: " precision step-lenght 1

  if not skip-dispersal-phase
  [
   if age-in-months < age-dispersal
   [
    ;; PUPS
    ; res-scale is the size of one patch in reality (m)
    set step-lenght random-normal (mean-speed-pups / resolution-scale) (sd-speed-pups / resolution-
scale)
   ]
  ]
    ;; to avoid seals taking a step backwards
    let min-step-lenght 0.1
    if step-lenght < min-step-lenght
    [
      set step-lenght min-step-lenght
    ]

end
;---------------------------------------------------------------------

to adjust-turning-angle

  set turning-angle random-normal mean-turning sd-turning

end

;---------------------------------------------------------------------

to set-exhaustion-rates

   ;; SWITCHES

   ;  without dispersal
  ifelse skip-dispersal-phase = true
  [
   set age-maturity 0
  ]
  [
   set age-maturity 48
   set age-dispersal 3
   ; Exhaustion rate NEWborns
```

```
   if age-in-months < age-dispersal
    [set exhaustion-rate exhaustion-rate-newborns]
   ; Exhaustion rate JUVENILE
   if (age-in-months >= age-dispersal) and (age-in-months < age-maturity)
    [ set exhaustion-rate (exhaustion-rate-adults * (age-in-months / age-maturity))]
  ]

  ; ADULT
  if age-in-months >= age-maturity
   [
    set exhaustion-rate exhaustion-rate-adults
   ]

end

;-----------------------------------------------------------------

to non-targeted-moving
  ;; MOVEMENT MODE 2

  ; chooses the turning angle, checks if land ahead
  ; if yes, it chooses the turning direction (avoid-land-decision) and turns as little as possible to avoid
the land
  right turning-angle
  see-if-land-ahead
  ifelse empty? is-land?
  [
    fd step-lenght
  ]
  [
    avoid-land-decision
  ]

end

;-----------------------------------------------------------------

to targeted-moving
;; MOVEMENT MODES 1 AND 3

;; find most attractive site
  if find-target = true
  [
    ;; Towards deep
    if movement-mode = 1
    [
      ; random deep patch in memory
      set target one-of deep-cors

      ;;OR CLOSEST DEEP (?):
      ; let distance-to-deeps []
```

```
    ; (foreach deep-cors [ set distance-to-deeps lput distance ?1 distance-to-deeps])
    ; let min-dis min distance-to-deeps
    ; let min-pos (position min-dis distance-to-deeps)
    ; set target (item min-pos deep-cors)
   ]

   ;; Towards haul out
   if movement-mode = 3
   [
    ifelse age-in-months > 3 and time >= warm-up and time <= warm-up + 0.5
    [
     go-home
    ]

    [
    ifelse age-in-months > 3
    ;; adults choose their haul out target based on distance and memory factor
    [
      calc-profitability-stones-past
    ]
    ;; newborns have only their birth lair as target site
    [
      set target old-home
    ; print target
    ]
    ]
   ]
   ;; target is set only in the beginning of modes 1 and 3
   set find-target false
  ]

;; -- IF LAND AVOIDANCE MODE ON--
  avoid-land


;; -- IF NO LAND AVOIDANCE MODE --
  ;; MOVE TOWARDS THE TARGET IF NO LAND AHEAD. OTHERWISE DECIDE TURNING MODE
  if avoidance-mode-right = false and avoidance-mode-left = false
  [
   set heading towards target
   right turning-angle

   see-if-land-ahead

   ifelse empty? is-land?
   [
    fd step-lenght
   ]
   [
    avoid-land-decision
   ]
```

```
  ]

end

;------------------------------------------------------------------

to avoid-land
 ;; -- TURN OFF LAND AVOIDANCE MODES --

    ;; Enables to turn off land avoidance mode if an island is already avoided
    if avoidance-mode-right = true or avoidance-mode-left = true
    [
    ;; turning-angle-target calculates what is the turning angle between the current heading
    ;; and towards the target
    ;; if small, most likely the island was already avoided

    set head-current heading
    set heading towards target
    let head-target heading
    let turning-angle-target (abs (head-target - head-current))

    ;; see if there is land ahead
    see-if-land-ahead

    ;; if there was land ahead, the island is still not avoided
    ;; but the turning-angle-target was due to a bay in an island
    ifelse empty? is-land?  and turning-angle-target <= 45
    [
      set avoidance-mode-left false
      set avoidance-mode-right false
    ]

  ;; Land avoidance modes are still on if island is still not avoided
  ;; keeping the land avoidance mode enables straight forward way of going around an island
  ;; otherwise the seal might get stuck to a bay if trying to reach a target

  ;; AVOID RIGHT
    [
      if avoidance-mode-right = true and avoidance-mode-left = false
      [
        avoid-land-right
      ]

  ;; AVOID LEFT

     if avoidance-mode-left = true and avoidance-mode-right = false
      [
        avoid-land-left
      ]
    ]
   ]
```

```
end

;---------------------------------------------------------------------------------
;; THIS IS TO IMPLEMENT LAND AVOIDANCE
;; makes a local list to check if land is ahead in step length or smaller.
;; smaller: needed so that the seal won´t jump over narrow land areas, step lenght can be > 1


to  see-if-land-ahead

  let check-land-distances
  (list
  (step-lenght)
  (step-lenght * 0.95)
  (step-lenght * 0.90)
  (step-lenght * 0.80)
  (step-lenght * 0.70)
  (step-lenght * 0.60)
  (step-lenght * 0.50)
  (step-lenght * 0.40)
  (step-lenght * 0.30)
  (step-lenght * 0.20)
  (step-lenght * 0.10)
  (step-lenght * 0.05))
  set is-land? []

  foreach check-land-distances
  [
    carefully
    [
     if ([land? = true] of patch-ahead ?)
     [
      set is-land? fput true is-land?
     ]
    ]
    [set is-land? fput true is-land?
     print "debug land nobody"]
  ]

end

;---------------------------------------------------

to calc-profitability-stones-past

  ;; calculate distances to haul out sites
  let dist-to-stonepos []
  (foreach stone-cors
   [
     set dist-to-stonepos lput (distance ?1 * resolution-scale) dist-to-stonepos
```

```
    ;;resolution scale transforms the distance to meters
   ]
  )

  ;; calculate attraction values
  let profits-list []
  (foreach memory-stones-list dist-to-stonepos
   [
    set  profits-list lput (?2 / ?1)  profits-list
   ]
  )

 ;; find the minimum value of the attraction list
 if not empty? stone-cors
 [
  let min-dist min profits-list
  let min-pos (position min-dist profits-list)
  set target (item min-pos stone-cors)
 ; print target
 ]

end

;-----------------------------------------------------------------------

to avoid-land-decision

 ;; AVOIDANCE MODE DECISION
 ;; Count how much is land in each side of the individual and avoid land where less

  set head-current heading

  ;; right side
  set count-right 0
  set heading (head-current + 45)
  set count-right count patches in-cone land-distance 90 with [land? = true]

  ;; left side
  set count-left 0
  set heading (head-current - 45)
  set count-left count patches in-cone land-distance 90 with [land? = true]

  ;; if equal amount of land patches, random selection
  if count-left = count-right
  [
   ifelse random-float 1 > 0.5
   [
    set count-right count-right + 1
   ]
   [
    set count-left count-left + 1
```

```
    ]
  ]

  ifelse count-left < count-right
  [
    ; choose left direction
    set heading head-current
    if movement-mode = 1 or movement-mode = 3
    [
      ;; keep the land avoidance mode until target can be reached freely in case of targeted moving
      ;; this way changing the direction while avoiding the same island is avoided
      set avoidance-mode-right false
      set avoidance-mode-left true
    ]
    avoid-land-left
  ]
  [
    ; choose right direction
    set heading head-current
    if movement-mode = 1 or movement-mode = 3
    [
      ;; keep the land avoidance mode until target can be reached freely in case of targeted moving
      ;; this way changing the direction while avoiding the same island is avoided
      set avoidance-mode-right true
      set avoidance-mode-left false
    ]
    avoid-land-right
  ]


end

;;------------------------------

to avoid-land-left
;; After making a decision to left OR in left land avoidance mode (possible in movement modes 1 and 3, targeted moving)
;; Adjusts the turning angle for avoiding the land from left side

  set heading head-current
  see-if-land-ahead
  set turning-counter 0
  ifelse empty? is-land?
  ;; If no land ahead and the seal wants to avoid the land from the left side,
  ;; it needs to turn "right" from current heading (clockwise). (makes the seal to follow the shoreline of an island)
  [
    let head-prev head-current
    loop
    [
      turn-clockwise
```

```
      see-if-land-ahead
      if not empty? is-land?
      [
        ;; When land encountered while turning, the seal knows that no more turning is needed
        ;; and it can choose the turning angle as the previous one
        set heading head-prev
        fd step-lenght
        stop
      ]
      if turning-counter = 36
      [
        ;; The step lenght is sometimes too small to encounter land.
        ;; If this happens, the seal can simply take a step towards target
        ;; as it went around 360 degrees already
        set heading towards target
        fd step-lenght
        stop
      ]

      set head-prev head-current
    ]
  ]
  ;; If there is land ahead and the seal wants to avoid the land from the left side,
  ;; it needs to turn left from current heading.
  [
    loop
    [
      turn-anticlockwise
      see-if-land-ahead
      if empty? is-land?
      [
        ;; When land is not encountered while turning, the seal knows that no more turning is needed
        fd step-lenght
        stop
      ]

      if turning-counter = 36
      [
        ;; The step lenght is sometimes too large and encounters always land.
        ;; If this happens, the seal can decrease the step lenght and start trying again
        set turning-counter 0
        set step-lenght step-lenght * 0.5
      ]
    ]
  ]

end

;------------------------------

to avoid-land-right
```

;; After making a decision to right OR in right land avoidance mode (possible in movement modes 1 and 3, targeted moving)
;; Adjusts the turning angle for avoiding the land from the right side

```
 set heading head-current
 see-if-land-ahead
 set turning-counter 0
 ifelse empty? is-land?
 ;; If no land ahead and the seal wants to avoid the land from the right side,
 ;; it needs to turn "left" from current heading. (makes the seal to follow the shoreline of an island)
 [
  let head-prev head-current
  loop
  [
   turn-anticlockwise
   see-if-land-ahead
   if not empty? is-land?
   [
    ;; When land encountered while turning, the seal knows that no more turning is needed
    ;; and it can choose the turning angle as the previous one
    set heading head-prev
    fd step-lenght
    stop
   ]

   if turning-counter = 36
   [
    ;; The step lenght is sometimes too small to encounter land.
    ;; If this happens, the seal can simply take a step towards target
    ;; as it went around 360 degrees already
    set heading towards target
    fd step-lenght
    stop
   ]
   set head-prev head-current
  ]
 ]
 ;; If there is land ahead and the seal wants to avoid the land from the right side,
 ;; it needs to turn right from current heading.
 [
  loop
  [
   turn-clockwise
   see-if-land-ahead

   if empty? is-land?
   [
    ;; When land is not encountered while turning, the seal knows that no more turning is needed
    fd step-lenght
    stop
   ]
```

```
      if turning-counter = 36
      [
        ;; The step lenght is sometimes too large and encounters always land.
        ;; If this happens, the seal can decrease the step lenght and start trying again
        set turning-counter 0
        set step-lenght step-lenght * 0.5
      ]
    ]
  ]

end

;--------------------------------------------------------------------------

to turn-clockwise
  ifelse head-current < 350
      [
        set head-current head-current + 10
        ;; increase of 10 degrees to the right
      ]
      [
        set head-current (head-current - 350)
        ;; if the degrees are already more than 350, need to start the circle from 0
      ]
      set turning-counter turning-counter + 1
      set heading head-current

end
;--------------------------------------------------------------------------

to turn-anticlockwise

  ifelse head-current >= 10
      [
        set head-current head-current - 10
        ;; increase of 10 degrees to the left
      ]
      [
        set head-current 360 - (10 - head-current)
        ;; if the degrees are already less than 10, need to start the circle from 360
      ]
      set turning-counter turning-counter + 1
      set heading head-current

end
;-------------------------------------------------------------------------


to sleep-in-water
```

```
  ; seal sleeps in the water if exhaustion 0.9999
  ;; INITIALIZE RESTING
  if exhaustion > 0.999 [set exhaustion 0.999]
  set movement-mode false
  set sleep-water true
  ;; deactivate previous target
  set target false
  set avoidance-mode-left false
  set avoidance-mode-right false
  set moving-dur 0

  ;;THE SEALS ARE RESTING UNTIL THE EXHAUSTION DECREASES ENOUGH
  set exhaustion exhaustion - (exhaustion-recovery-rate * exhaustion * (1 - (exhaustion / 1)))
  if exhaustion < moving-threshold
  [
    set sleep-water false
  ]

end

;-------------------------------------------------------------------------------

to remember-deep

  if (deep = true)
  [
    set deep-cors fput patch-here deep-cors
    set deep-cors remove-duplicates deep-cors
    if target != false
    ;; decreases the step length if distance to target is smaller
    [
      if distance target  <= step-lenght
      [
        set step-lenght distance target
        set heading towards target
        fd step-lenght
        set movement-mode 2
        set target false
        ]
    ]
  ]

  if length deep-cors = 100
  [
    set deep-cors remove (last deep-cors) deep-cors
  ]

end
;-------------------------------------------------------------------------------

to list-coordinates
```

```
let write_prob random-float 1

; add x and y coordinates to coordinate lists
; make 3 x y points for haul outs
; that the model does not produce biased results (emphazising the relocations when moving)
ifelse movement-mode = false
[
  ; 1st
  set X lput xcor X
  set Y lput ycor Y
  ; give age as months
  set age-locations lput ((2 / 3) / 24 / 30) age-locations

  ; 2nd
  set X lput xcor X
  set Y lput ycor Y
  ; give age as months
  set age-locations lput ((1 / 3) / 24 / 30) age-locations

  ; 3rd
  set X lput xcor X
  set Y lput ycor Y
  ; give age as months
  set age-locations lput ((0 / 3) / 24 / 30) age-locations
]
[
  if write_prob < 0.25
  [
  set X lput xcor X
  set Y lput ycor Y
  set age-locations lput 0 age-locations
  ]
]

;; age-locations - to match coordinates to evaluation season
;; update "age" of locations
let age-locations-temp []
(foreach age-locations
  [
    ;; in every tick the age of the location increases, age given as months
    set age-locations-temp lput (? + (1 / to-hours-scale / 24 / 30)) age-locations-temp
  ]
 )
set age-locations age-locations-temp

;; skip winter season (Dec-April) locations as the time skips it too
if time = floor 9 or remainder (floor time - 9)(12) = 0
[let age-locations-temp2 []
 (foreach age-locations
```

```
    [
     set age-locations-temp2 lput (? + 4) age-locations-temp2
    ]
    )
    set age-locations age-locations-temp2
   ]

   ;; delete location data bigger than evaluation season
   foreach age-locations
   [
     if ? > evaluation-season
     [let removable-loc position ? age-locations
      set X remove-item removable-loc X
      set Y remove-item removable-loc Y
      set age-locations remove-item removable-loc age-locations]
   ]


end
;-----------------------------------------------------------------------------

;-----------------------------------------------------------------------------
;; PLOTS

to report-distance-travelled

   ask seals
   [
     set step-taken distance loc-prev
     set loc-prev patch-here
     ;; distance from home
     set distance-from-home ((distance old-home) * resolution-scale / 1000)
   ]

end


to plot-haul-out-duration

  set-current-plot "Haul-out duration [red] and moving duration [blue]"
  ask seals
  [
   set-current-plot-pen "Moving duration"
   set-plot-pen-color blue
   set-plot-pen-mode 2
   plotxy ticks moving-dur

   set-current-plot-pen "Haul-out duration"
   set-plot-pen-color red
   set-plot-pen-mode 2
   plotxy ticks haul-out-dur
```

```
  ]

end

to plot-distance-from-home

  set-current-plot "Distance from home"
  ask seals
  [
    set-current-plot-pen "Distance from home"
    set-plot-pen-color black
    set-plot-pen-mode 2
    ;; change first to meters with resolution scale and then to km, dividing by 1000
    plotxy ticks distance-from-home
  ]

end

;;------------------------------------------------------------------------------

to pen-down-illustration
  ask seals [pen-down]

;  if color-coding
;  [
    ask seals
    [
      if age-in-months < age-dispersal
       [set color 105]
      if age-in-months > age-dispersal
       [set color 115]
      if age-in-months > age-maturity
       [set color 15]
;      if color-evaluation-season
;      [
;       if (time + evaluation-season) > run-time
;       [set color red]
;      ]
    ]
;  ]

end

;;------------------------------------------------------------------------------
to write-results

  if write-results-file
  [
```

```
   let write_prob random-float 1 ; This was done so that the number of datapoints for distance from
home would match better
                    ; to the dataset of calibration individual ER11


;; OUTPUT FILE CONTAINING ONLY DISTANCE FROM HOME

   let file-name-2 (word "Dist_home" ".csv")

;    let file-name-2 (word "Dist_home-" "-" behaviorspace-run-number ".csv")
   file-open file-name-2
   ifelse movement-mode = false
   [
;      file-type (word run-number ",")
;      file-type (word mean-speed-adults ",")
     file-print (word distance-from-home ",")

   ]
   [
     if write_prob < 0.45
     [
;       file-type (word run-number ",")
;       file-type (word mean-speed-adults ",")
       file-print (word distance-from-home ",")

     ]
   ]

   file-close

;; OUTPUT FILE CONTAINING ONLY MOVING DURATION

   let file-name-3 (word "Mov_dur" ".csv")
;    let file-name-3 (word "Mov_dur-" "-" behaviorspace-run-number ".csv")
   file-open file-name-3

   if moving-dur_report > 0
   [
;      file-type (word run-number ",")
;      file-type (word mean-speed-adults ",")
     file-print (word moving-dur_report ",")
   ]
   file-close

  ]


end

;;--------------------------------------------------------------
```

```
;; HOME RANGES
to calc-homerange

  ask seals
   [
     pen-up
     let temp-list-XY (map [list ?1 ?2] X Y)

     ;; X and Y to form patch-set "my-patches"
     foreach temp-list-XY
     [
     set my-patches (patch-set patch (item 0 ?) (item 1 ?) my-patches)
     ]

     ;; calc a
     foreach temp-list-XY
     [
        move-to patch (item 0 ?) (item 1 ?)
        let max-patch one-of my-patches with-max [distance myself]
        set distances fput distance max-patch distances
        set a max distances
     ]
     ; transform a to [m]
     set a (a * resolution-scale)

     ;; write the ouput file with the locations' coordinates
     if write-coordinates
     [
       let output-file-name (word "Coordinates" ".csv")
       file-open output-file-name
       foreach temp-list-XY
       [
         move-to patch (item 0 ?) (item 1 ?)
         let X.meters (item 0 ?) * resolution-scale
         let Y.meters (item 1 ?) * resolution-scale
         file-type X.meters file-type ","
         file-type Y.meters file-type ","
         file-print who
       ]
       file-close
     ]
   ]

end

;;----------------------------------------------------------------------------


to go-home

  ask seals
```

```
  [
    set target old-home
;    print "I'm going home!"
;    print target
;    print time - warm-up
  ]

end
```