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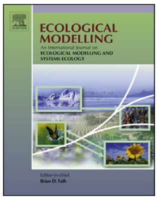

# Modelling movements of Saimaa ringed seals using an individual-based approach

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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.

## 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).

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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 9500 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 1300 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 et al., 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 ($\geq$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), physiolog-