



Linking Movement Ecology with Wildlife Management and Conservation

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A common challenge in species conservation and management is how to incorporate species movements into management objectives. There often is a lack of knowledge of where, when, and why species move. The field of movement ecology has grown rapidly in the last decade and is now providing the knowledge needed to incorporate movements of species into management planning. This knowledge can also be used to develop management strategies that are flexible in time and space and may improve the effectiveness of management actions. Therefore, wildlife management and conservation may benefit by strengthening the link with movement ecology. We present a framework that illustrates how animal movement can be used to enhance conservation planning and identify management actions that are complementary to existing strategies. The framework contains five steps that identify (1) the movement attributes of a species, (2) their impacts on ecosystems, (3) how this knowledge can be used to guide the scale and type of management, (4) the implementation, and (5) the evaluation of management actions. We discuss these five steps in detail, highlighting why the step is important and how the information can be obtained. We illustrate the framework through a case study of managing a highly mobile species, the Atlantic salmon (*Salmo salar*), a harvested species of conservation concern. We believe that the movement-management framework provides an important, and timely, link between movement ecology and wildlife management and conservation, and highlights the potential for complementary, dynamic solutions for managing wildlife.

Keywords: adaptive management, animal movement, conservation, movement ecology, wildlife management

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INTRODUCTION

The field of movement ecology has grown rapidly in the last decade due to a number of recent technological and analytical advances in tracking animal movement (Tomkiewicz et al., 2010). Alongside the growth in technological advances have been advances in conceptual frameworks that aim to unify research in animal movement (Nathan et al., 2008) and incorporate movement into biodiversity research (Jeltsch et al., 2013). This growth has provided a number of benefits for conservation and management, such as improving our understanding of habitats important for wildlife and the area traversed by wide-ranging species (Hebblewhite and Haydon, 2010). However, it has also highlighted a number of challenges for conservation, such as maintaining connectivity, both within the landscape and for species with wide-ranging movements like nomadic or migratory species (Sanderson et al., 2002; Martin et al., 2007; Runge et al., 2014). At the same time, studies have

revealed that traditional approaches to conservation, such as protected areas, may be inadequate due to reasons like the spatial scale of a species movements (e.g., Thirgood et al., 2004), conflicts with stakeholders (e.g., Symes et al., 2015), or available finances (e.g., Carwardine et al., 2008; Chadés et al., 2015). Traditional approaches will continue to have a vital role in conservation planning, however their effectiveness may be improved if they are combined with strategies that are flexible in time and/or space (Runge et al., 2014; Chadés et al., 2015; Tulloch et al., 2015).

Research in movement ecology is generating knowledge of species movements that enables managers to implement actions that are flexible in space and time. As a result, managers have begun to link the movement ecology of a species with management planning, resulting in targeted management actions that incorporate species movements or specific areas where threats are located (Table 1). An example is how the results of a tracking study for leatherback turtles (*Dermochelys coriacea*) were used to identify new potential conservation strategies to reduce leatherback-fisheries interactions that included targeted spatial actions and dynamic time-area closures along the migration corridor (Table 1; Shillinger et al., 2008). Knowledge of species movements is also being used to prioritize management actions and achieve maximum benefit from the limited funds available (Martin et al., 2007; Carwardine et al., 2008, 2012). An example is focusing management actions on bottleneck sites, which are particular areas that species rely upon like stopover sites (Iwamura et al., 2014), or where landscape connectivity is being constrained by physical barriers (Table 1; Sawyer et al., 2013; Seidler et al., 2015). These studies highlight the potential for linking management planning with movement ecology. However, the examples are few and greater emphasis is needed to link the fields of movement ecology and conservation if we are to improve upon the existing model.

We formulated a conceptual Movement-management framework (hereon described as framework) to illustrate how knowledge of animal movement may enhance management planning. The workflow described in the framework is applicable across taxa, as many species exhibit movements that vary from being sedentary year round, to migration, nomadism, and dispersal (Table 1). Furthermore, these movements share common attributes across taxa, such as the use of pathways, stopover sites, seasonal ranges, or breeding sites. We outline the steps used in the framework, their rationale and highlight some aspects that require important considerations. We discuss its implementation, how it links to existing practices and identify potential challenges for its implementation. Through a case study of the Atlantic salmon (*Salmo salar*), we show how knowledge of movement has been used and can be used further to guide management planning.

MOVEMENT-MANAGEMENT FRAMEWORK

The framework is organized into five interlinked steps, whereby baseline information on species movements are used to guide management decisions (Figure 1). The first three steps include understanding species' movements, their ecosystem impacts and how these are linked to the scale of management required

(Figure 1). A fourth step considers the implementation of management actions whilst the final step incorporates an adaptive management component of evaluation (Figure 1).

The primary requirement for the framework is the availability of animal movement data that is appropriate for the management objective(s). The movement data required will depend upon the ecological or conservation questions underlying the management objectives, and may involve considerations like whether the time period of observation is long enough to make general conclusions on movement patterns, or whether the sample size is large enough to make population level inferences (Figure 1). In addition, quantitative methods for analysing movements have progressed rapidly with time (Patterson et al., 2008; Kranstauber et al., 2012; Fleming et al., 2015). These methods have specific requirements regarding the quality of data needed, as few as 10 locations per month may be sufficient to estimate a home range but this would not be sufficient for understanding resource use (Marzluff et al., 2004; Börger et al., 2006). However, it should be noted that detailed movement data is not always available. Instead, informed decisions can be made based on predictive modeling that are performed in conjunction with alternative sources of data, such as expert opinion or presence data (Low Choy et al., 2009; Iwamura et al., 2014). These data sources may guide initial decision making processes whilst more detailed data are acquired (Grantham et al., 2009), and may also benefit study design by identifying existing knowledge gaps. Collecting new movement data may be limited by the study species, available time, or money. Nevertheless, the improved knowledge that movement data provides may lead to more effective management actions as opposed to costly mistakes (Carwardine et al., 2008; Grantham et al., 2009).

Movement Attributes

The target for managers is to develop an understanding of how individual movements affect a species survival and reproduction and therefore population dynamics. An individual's decision to move is influenced by several factors that include food resource availability and/or quality, predator avoidance and environmental conditions, which will enhance its capacity to survive and reproduce (Morales et al., 2010; van Moorter et al., 2013). Movement attributes, like the timing of spring migration, may have direct effects on the fitness of individuals (Winkler et al., 2014). A number of bird species have not advanced the timing of their spring migrations in response to climate change, and appear to be declining because the timing of breeding has become mismatched with peak food availability (Møller et al., 2008). Furthermore, the performance of a population may also be influenced by the ability of individuals to adapt their movements to environmental change, such as adapting foraging movements to habitat loss (McNamara et al., 2011; Winkler et al., 2014).

Applying the first step of the framework allows managers to identify how animal movements influence demography and subsequent population dynamics (Figure 1). Animal movement can be described according to three major population-level distribution strategies that include being sedentary in annual ranges, migration and nomadism (Mueller and Fagan, 2008). Being sedentary on an annual scale involves having stable home

TABLE 1 | Links between movement ecology and wildlife management.

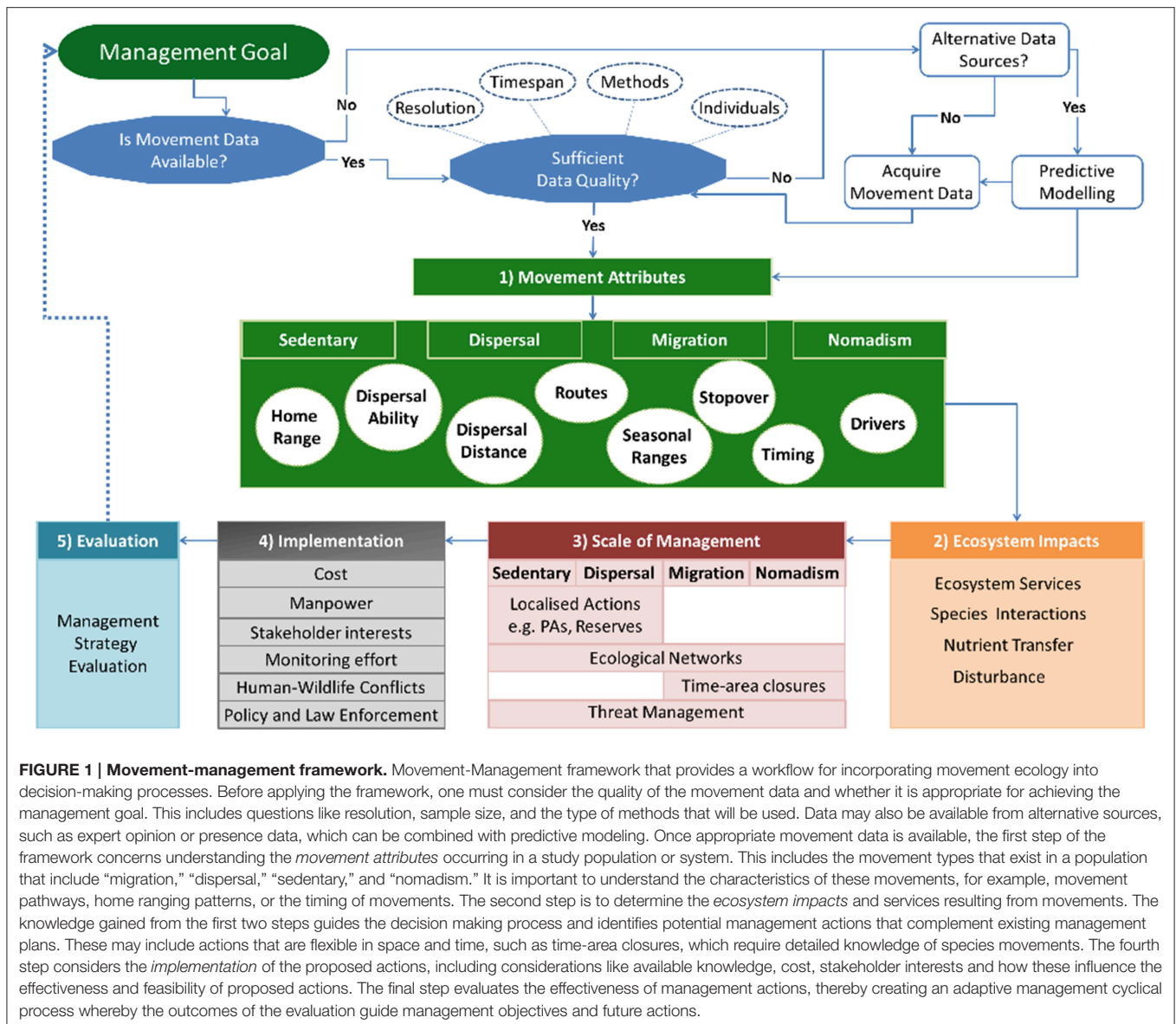
Taxa	Movement attributes	Ecosystem impacts	Scale of management	Source
BIRDS				
New World land birds	Migratory Scale and Timing	Services (pest predation)	Ecological Networks (stopover, summer/winter)	Martin et al., 2007; Kellermann et al., 2008; Faaborg et al., 2010
Waterfowl	Migratory Timing	Seed Dispersal; Aggregative impacts, Disease transmission	Temporary wetlands Ecological networks,	Kerbes et al., 1990; Figuerola and Green, 2002; O'Neal et al., 2008; Altizer et al., 2011
Greater sage-grouse (<i>Centrocercus urophasianus</i>)	Sedentary/Migratory Scale, Timing, and Drivers	Trophic level (umbrella species), Nutrient transfer	Localized Actions	Rowland et al., 2006; Dzialak et al., 2011; Fedy et al., 2012
MAMMALS				
Woodland/Mountain Caribou (<i>Rangifer tarandus caribou</i>)	Migratory Scale, Timing, and Drivers	Nutrient Transfer; Direct use; Ecosystem Indicator	Ecological Network Temporary	Ferguson and Elkie, 2004; Johnson et al., 2004; Saher and Schmieglow, 2004; Pinar et al., 2012
Saiga (<i>Saiga tatarica</i>)	Migratory Scale and Timing	Nutrient Transfer; Potential for Direct use	Temporary (Proposed) Threat management	Milner-Gulland, 1997; Singh and Milner-Gulland, 2011; Bull et al., 2013
Wildebeest (<i>Connochaetes taurinus</i>)	Sedentary/Migratory Scale and Drivers	Nutrient Transfer; Direct use	Localized Actions (PA)	Thirgood et al., 2004; Holdo et al., 2010
Mule deer (<i>Odocoileus hemionus</i>)	Migratory Scale, Timing, and Drivers	Nutrient cycling; Direct Use; Seed Dispersal	Ecological Networks (Connectivity)	Myers et al., 2004; Monteith et al., 2011; Sawyer and Kauffman, 2011
Mongolian gazelle (<i>Procapra gutturosa</i>)	Nomadic Scale and Drivers	Nutrient Transfer	Temporary	Mueller et al., 2008; Sawyer et al., 2013
FISH				
Near-shore species	Sedentary Scale	Regulatory services, nutrient transfer, trophic level	Ecological Network, Size of reserve	Holmlund and Hammer, 1999; Moffitt et al., 2009; Gaines et al., 2010
Bluefin tuna (<i>Thunnus spp.</i>)	Migratory Scale, Timing, and Drivers	Trophic level, nutrient transfer	Temporary	Armstrong et al., 2010
INSECTS				
Monarch butterfly (<i>Danaus plexippus</i>)	Migratory Scale and Drivers	Services (Cultural, pollination), Ecotourism	Ecological network (connectivity of wintering and breeding sites, pathway)	Barkin, 2003; Howard and Davis, 2009; López-Hoffman et al., 2010; Brower et al., 2012
Dragonfly spp.	Migratory Drivers	Trophic Level	Ecological Network, Temporary	Wikelski et al., 2006; Hobson et al., 2012
REPTILES				
Leatherback Sea Turtle (<i>Dermochelys coriacea</i>)	Migratory Scale, Timing, and Drivers	Trophic Level	Temporary Threat management	Sherrill-Mix et al., 2008; Shillinger et al., 2008; Fossette et al., 2010

Examples from the literature where aspects of the movement-management framework have been applied. The species in focus are from varying taxonomic groups that include mediums of travel on the ground, in air and water. The movement attributes were summarized into the type of movement (sedentary, migratory, nomadic) and what is known about the species' movements, namely "Scale"—distance of movements and knowledge of space use, "Timing"—when movements occur or "Drivers"—factors influencing movement like habitat, cues or predators. Ecosystem Impacts describe both the services a species may provide and the potential impacts of their movements. The scale of management indicates the current or recommended management actions—the term "Temporary" refers to any temporary form of management such as time-area closures. The studies listed in source are referenced in Appendix A.

ranges or territories, where an individual occupies a relatively small area compared to the population distribution (Mueller and Fagan, 2008). Migration consists of seasonal, round-trip movements between spatially disjunct areas (Mueller and Fagan, 2008; Harris et al., 2009). Nomadism differs from being sedentary or migratory as individuals move across the landscape using routes that do not repeat across years (Mueller and Fagan, 2008). A fourth movement type that managers need to consider is dispersal. Dispersal is the movement to a site of reproduction and includes movements away from the site of birth (natal dispersal) and movements between successive reproductive sites (breeding dispersal; Matthysen, 2012). The types of movements present in the population will influence the type of management

actions needed, such as preserving connectivity for dispersing and nomadic movements, setting aside reserves for species which are sedentary in their annual home ranges or adopting a flyway approach for conserving migratory species (Klaassen et al., 2008; Howard and Davis, 2009; Minor and Lookingbill, 2010; Hodgson et al., 2011). Previous research has shown that management interventions have been less effective when management actions have not matched the spatial, or temporal, scale of species movements (Thirgood et al., 2004; Moffitt et al., 2009).

In addition to the types of movement present in the population, it is important to understand the characteristics of movements. These comprise of movement pathways, distance and timing of movements, shapes and sizes of home ranges,



habitat selection along movement paths and the use of stopover sites by migratory species (Figure 1). Understanding the type of movement in the population determines the types of management actions needed, but understanding the characteristics of movements is necessary for planning, designing, and implementing management actions. For example, understanding movement pathways is particularly important when managers aim to maintain connectivity, particularly as the loss of some sites can lead to sudden population decline (Webster et al., 2002; Iwamura et al., 2013). Movement pathways also indicate whether species use matrix habitats (Fischer et al., 2005), are restricted to specific habitat types (Hagen et al., 2012), or barriers prevent movements (Sawyer et al., 2013). Other movement characteristics, such as the size and shape of home ranges, are often used to guide the scale of management (Schwartz, 1999) and to determine habitat preference and

subsequent habitat suitability (Chetkiewicz and Boyce, 2009; Lu et al., 2012). Knowledge of movement characteristics may also identify potential threats, such as the increased risk of exploitation due to the predictable and aggregating nature of some migratory species (Bolger et al., 2007; Harris et al., 2009). We expand upon how knowledge of the types and characteristics of species movements can be used to guide the scale of management in Section Scale of Management.

Ecosystem Impacts

Animal movement is a core component of an ecosystem and maintaining movement patterns may be vital for sustaining ecosystem processes like trophic and species interactions (Lundberg and Moberg, 2003; Massol et al., 2011). Movement provides links between ecosystems and these links may be classified as either resource, genetic or process links (reviewed

in Jeltsch et al., 2013). The frequency and type of link will be affected by the spatiotemporal scale of movement, such as foraging movements within the home range or the less frequent but larger scale movements of migration (Jeltsch et al., 2013). Movement is also important for maintaining interaction networks in both antagonist (e.g., predator-prey) and mutualist (e.g., plant-pollinator) networks (Tylianakis et al., 2010; Hagen et al., 2012). The loss of species interaction networks may have cascading effects on for example food web dynamics resulting in secondary extinctions (Hagen et al., 2012). Managers also need to consider how movement may disturb ecosystems. The aggregating nature, and long-range movements, of many migratory species may impact ecosystems through exploitation of habitats, disease transmission and nutrient loading (Kerbes et al., 1990; Post et al., 2008).

Animal movement may provide important ecosystem services and these services have been termed *mobile-agent based ecosystem services* (MABES; Kremen et al., 2007). These services are provided at a local scale by species moving within or among habitats (Kremen et al., 2007). For example, the movements of bees pollinate both wild and agricultural plants (Kremen et al., 2007), seeds may be dispersed long distances by birds and mammals (Nathan and Muller-landau, 2000) and nutrients are transferred between marine and terrestrial environments by the foraging movements of seabirds (Ellis et al., 2006). The ongoing modification of the landscape by humans is altering landscape connectivity and threatens the future provision of MABES (Mitchell et al., 2013). Linking animal movement with management planning allows managers to identify the ecosystem functions and services that movement provides and thus improve landscape management (Jeltsch et al., 2013; Mitchell et al., 2013).

Scale of Management

A challenge for management is identifying the scale of management required for effective species conservation. The scale of management may be guided by, amongst others, the distance of movements like migrations (Klaassen et al., 2008), by the size of home ranges (Schwartz, 1999), or by the habitat requirements of a species (Angelstam et al., 2004). Habitat selection studies have commonly been used to identify the habitat requirements of a species, in particular using the four orders of habitat selection described by Johnson (1980). The first-order of selection identifies the geographical range of the species and has commonly been used to map species distributions and develop habitat suitability models, which are used to guide the scale of conservation planning (Johnson, 1980; Angelstam et al., 2004; Guisan et al., 2013). The second, third and fourth orders of selection concern the selection of the home range, habitat patches within the home range and microhabitats within used patches respectively (Johnson, 1980; Meyer and Thuiller, 2006). Meyer and Thuiller (2006) introduce a fifth order of selection, which are areas used by populations within the geographical range. These orders of selection inform managers about local reserve site selection (Aldridge and Boyce, 2007; Guisan et al., 2013), provide indications of habitat quality and improvements needed (e.g., Dickson and Beier, 2002; Zeale et al., 2012) and how human disturbance may

be influencing species movements (e.g., Hornseth and Rempel, 2015). However, an ongoing challenge in conservation is how to achieve the scale of management required. Knowing species movements answers important management questions like where, when, how and why animals move, which can be used to develop management actions that increase the dynamism and scale of wildlife management, and are complementary to existing plans. Alternative management actions may include ecological networks, time-area closures or threat management, and we expand upon these alternative management actions below.

The first approach is concerned with incorporating localized management actions, such as protected areas or reserves, into a network of areas and thus increasing the scale of management. Ecological networks should maintain ecosystem processes, which includes the movement of organisms and subsequent species interactions networks (Opdam et al., 2006; Hagen et al., 2012). Ecological networks also incorporate multiple objectives into the spatial planning process, such as conservation goals and different land uses by stakeholders (Opdam et al., 2006). A principal concept of ecological networks is connectivity, whereby a set of areas or ecosystems are linked to maintain or enhance population viability by facilitating movement (Beier, 1998; Opdam et al., 2006). Management tools used to improve connectivity of two or more areas are matrix management and corridors (Beier, 1998; Fischer et al., 2005). Identifying which habitats are important for species helps managers create a “soft,” more permeable matrix. For example, a matrix containing scattered trees facilitated the movement of birds in Australia (Fischer et al., 2005). Habitat patches may also act as important stepping stones for long-distance dispersal and range expansions, following climate-driven shifts in habitat suitability (Saura et al., 2014). Strengthening the link between corridor design and species movements improves connectivity in the landscape, for instance, corridors that were identified through tracking studies were more effective than those identified through modeling approaches (LaPoint et al., 2013). Corridors may be beneficial for species moving at larger scales like the Mule deer *Odocoileus hemionus* R., for maintaining connectivity within a species home range, and to preserve dispersal events and maintain functional connectivity (Table 1; Baguette and Van Dyck, 2007; LaPoint et al., 2013; Sawyer et al., 2013).

The second approach is the use of time-area closures. Time-area closures may be dynamic in time only, i.e., excluding unwanted practices during a specific time of year, such as a stopover site for migratory waterfowl (O’Neal et al., 2008). Time-area closures may also be dynamic in space and time, i.e., the closure tracks the species’ movements like the movements of pelagic species (Hobday and Hartmann, 2006). Time-area closures provide a viable alternative for managing species’ with predictable movements. They can be implemented when species are most vulnerable, such as aggregation or spawning areas and during critical movement phases (Table 1; Hunter et al., 2006; Shillinger et al., 2008; Bull et al., 2013). Time-area closures may also achieve conservation targets whilst incorporating stakeholder interests, for example by maintaining alternative land-use or harvesting practices, and are being increasingly

utilized in marine and freshwater ecosystems (Hobday and Hartmann, 2006; O'Neal et al., 2008; Shillinger et al., 2008).

When it is not possible to spatially delineate large areas, it may be more appropriate to manage the primary threats to a species instead (Carwardine et al., 2012). Understanding a species' threats enables managers to prioritize management actions that achieve the greatest impact (Auerbach et al., 2014; Tulloch et al., 2015). Identifying threats to a species may also indicate which movement attributes increase species vulnerability. Traits of some species, such as the predictability of routes, timing of movements, or reliance upon particular sites may increase the risk of exploitation (Bolger et al., 2007). This knowledge can be used to guide management decisions, for instance threat management actions may involve time-specific interventions like anti-poaching activities at important locations and times of the year (Berger et al., 2008; Murgui, 2014). Recent advances in tracking technologies also provide the opportunity to incorporate real-time monitoring data into threat management schemes, thus justifying the cost of tracking animal movements (Wall et al., 2014). Real-time tracking data from African elephants *Loxodonta africana* in Kenya was used to notify wildlife managers when elephants were about to move into community areas (Wall et al., 2014). Wildlife managers were able to intervene and prevent the elephants causing crop damage and reduce human-wildlife conflicts, a major threat to elephants in Africa (Wall et al., 2014).

Implementation

The feasibility of management actions described above may be limited at the implementation phase by considerations like costs, stakeholder interests, and enforcement. Incorporating animal movement into management planning may entail a number of costs, such as the costs of acquiring land and the costs associated with establishing and maintaining a network of managed areas (Naidoo et al., 2006). Emphasis is now being placed on identifying the most cost effective action that maximizes benefits (Naidoo et al., 2006; Carwardine et al., 2012; Auerbach et al., 2014). The interests of local stakeholders may also influence the implementation of management actions due to conflicts between involved parties, for example conflicts arising over land-use, resettlement, policies or legislation, and human-wildlife conflicts (Davies et al., 2013; Symes et al., 2015). In addition, limitations may arise due to available manpower, either in relation to monitoring the outcomes of management actions or enforcing them (Keane et al., 2008). These challenges are especially pertinent when a species' movements takes them across several country borders (Iwamura et al., 2014; Kark et al., 2015). Cross-boundary collaborations may provide a number of benefits, such as improving the cost effectiveness of management actions and increasing the scale of threat management, however it also presents a number of challenges like political instability, increased costs related to establishing the collaboration, conflicting national goals, and potential delays in implementing actions (Kark et al., 2009, 2015). However, incorporating the above challenges into the decision making process allows managers to identify management strategies that are implementable and attainable.

A number of approaches have been developed to identify which management actions will maximize benefits, such as decision theoretic approaches and systematic conservation planning (e.g., Margules and Pressey, 2000; Wilson et al., 2009). Decision theoretic approaches consist of an objective or desired outcome, a description of our knowledge of the system, state variables in the area of interest, such as species populations or habitats, control variables which represent possible management strategies, model constraints and an equation that describes the relationship between the benefit of actions and the potential management strategies in the area of interest (Wilson et al., 2009). Understanding species movements enables managers to improve their understanding of the threats, use their knowledge of where and when a species will be to identify alternative management actions, and also recognize the challenges of achieving the management objectives which may not be apparent if a species' movements are unknown. Decision theoretic approaches enable managers to prioritize management actions that will better achieve the management objectives (Tulloch et al., 2015). Previously, actions were prioritized on areas with the highest threats or species richness, but now the management actions themselves are being prioritized depending upon whether they are cost-effective, have the greatest impact and are achievable (Auerbach et al., 2014; Tulloch et al., 2015). Multiple-action prioritization schemes are also being considered, whereby a combined set of strategies may be more cost effective and have greater impact than any one strategy alone (Wilson et al., 2009; Chadés et al., 2015). Therefore, it is vital for managers to evaluate all possible management scenarios to improve the effectiveness of the decision-making process.

Evaluation

The importance of evaluating management actions has been highlighted in recent decades to avoid implementing management actions that do not achieve management goals and thus waste limited funds (e.g., Ferraro and Pattanayak, 2006; Walsh et al., 2012). Therefore, management strategy evaluation (MSE) is vital for determining whether actions have either succeeded or failed in achieving the management objective, and using this knowledge to inform future decisions and actions (Pullin et al., 2013). Evaluation is an integral part of adaptive management and is thus applicable to any form of wildlife management. With regards to our framework, evaluation may be important for determining the effectiveness of actions implemented with incomplete knowledge of species movements, and may help prioritize the type of knowledge needed to improve future management. Evaluation is also important for tracking future uncertainties, such as how variation in the timing of movement may affect management strategies like time-area closures, which rely upon knowledge of where and when a species will be.

The effectiveness of management actions can be simulated prior to their implementation, through frameworks like the MSE framework (Smith et al., 1999), which has thus far been used mostly in commercial fisheries but also has relevance for the management and conservation of terrestrial species (Bunnefeld et al., 2011; Milner-Gulland, 2011). MSE compares multiple

management strategies prior to their implementation, allowing managers to identify their effectiveness and understand the varying forms of uncertainty, such as incomplete knowledge of species movements (Bunnefeld et al., 2011). The outcomes of MSE are used to inform the management objectives, study design, and implementation of management actions (Bunnefeld et al., 2011; Milner-Gulland, 2011). For example, comparative analyses could be performed to determine whether management actions should be implemented with limited knowledge of movement or whether priority should instead be placed on acquiring data that can be used to develop management actions that are more tailored to species movements and consequently have greater impact, such as those developed for the leatherback turtle discussed earlier (Shillinger et al., 2008).

APPLYING THE MOVEMENT-MANAGEMENT FRAMEWORK

We illustrate the potential for linking movement ecology with management through a case study of the Atlantic salmon. By following the steps of the framework, we show how existing knowledge of salmon movement ecology has been used to develop management actions and how further knowledge could be used to identify alternative management actions.

Case Study—Managing Atlantic Salmon (*Salmo salar*) in the Baltic Sea Background

Atlantic salmon have had large population declines in the Baltic Sea (Karlsson and Karlstr rn, 1994; Klemetsen et al., 2003) so it is an important issue for management and conservation alike. Overfishing and the loss of connectivity in river systems, due to hydroelectric dams, has been a driving cause of salmon declines and in the 1990s only 12 of the 44 naturally reproducing salmon stocks in the Gulf of Bothnia remained (Karlsson and Karlstr rn, 1994). A number of actions have been taken to restore these populations but several rivers are not self-sustaining and many salmon rivers are below 50% of potential smolt production (ICES, 2012). In this case study, we focus on the management goals of the Swedish government, through the Swedish Agency for Marine and Water Management (SwAM). Their aim is to reverse the decline of salmon stocks whilst maintaining activities like recreational and commercial fishing. Multiple techniques have been used to monitor the movements of salmon that include observational and trapping data (Lundqvist et al., 2010), tagging methods (Payne et al., 2010), acoustic or radio telemetry (Serrano et al., 2009), stable isotopes, and genetics (Barnett-Johnson et al., 2008). Therefore, several sources of movement data are available to continue with the movement-management framework.

Step 1—Movement Attributes

Salmon can exhibit all four types of movement (sedentary, dispersal, nomadism, and migration) during its life cycle. Salmon hatch in freshwater rivers, where they are solitary and defend territories for food, thus exhibiting sedentary movements (Lundqvist, 1983). During this phase they may also disperse

to nearby tributaries (McCormick et al., 1998). After 1 to 5 years the salmon migrates downstream to enter the sea (Lundqvist, 1983; Otero et al., 2014). Salmon movements in the sea remain difficult to study but this phase can be described as nomadic where the distribution of salmon is largely influenced by environmental factors like sea temperature, surface currents, and food availability (Klemetsen et al., 2003; Trudel et al., 2011). Salmon from multiple river systems mix in the Main Basin of the Baltic Sea, leading to mixed-stock fisheries (Karlsson and Karlstr rn, 1994). Salmon normally migrate back to their natal river systems to spawn (Lundqvist, 1983). The movements of hatchery-reared salmon may differ from wild salmon in their extent, timing, and fidelity (McKinnell et al., 1994; Jutila et al., 2003).

Step 2—Ecosystem Impacts

The stage-structured life cycle of salmon means that juveniles and adults occupy and connect different ecosystems (Schreiber and Rudolf, 2008; Miller and Rudolf, 2011). Species with complex life cycles may cause abrupt changes in different ecosystems, such as how changes in juvenile abundance may lead to trophic cascades across ecosystems to the adult habitat (Knight et al., 2005; Schreiber and Rudolf, 2008). The salmon's life cycle influences food web dynamics by preying on aquatic species and being preyed upon by aquatic, terrestrial, and avian species (Holmlund and Hammer, 1999, 2004). The Atlantic salmon is iteroparous, meaning it can spawn repeatedly as opposed to dying after spawning like the semelparous Pacific salmon (*Oncorhynchus spp.*; Klemetsen et al., 2003). Salmon deaths, and repeated migrations, link ecosystems and transfer nutrients and carbon between marine and freshwater ecosystems (Holmlund and Hammer, 1999, 2004). Salmon provide several ecosystem services. Spawning salmon regulate sediment processes whilst their movements between marine and freshwater ecosystems support aquatic/terrestrial food webs and nutrient cycling (Bottom et al., 2009; Kulmala et al., 2012). Salmon populations provide a highly valued food source for both commercial, personal-use, and recreational fisheries (Kulmala et al., 2012).

Step 3—Scale of Management

The life cycle of the salmon illustrates the importance of understanding their movements due to the direct influence that salmon movement has on their survival and reproduction. As a consequence, the scale of management may vary in accordance to the specific life cycle stage and process that is being targeted by management. For instance, management may consider the implementation of more localized management actions during the sedentary phases of the salmon's life cycle. These include the development phase after hatching salmon and spawning phase of adults. Management actions have therefore focused on either preserving existing habitats used by salmon, or alternatively, restoration actions have been taken to improve habitat suitability for spawning and recently hatched salmon (Nilsson et al., 2005).

A key aspect of salmon movements is the migration from the natal/spawning areas to the sea and their return to rivers. Lundqvist et al. (2008) indicate that a salmon population could increase by 500% if connectivity was improved along

the migration path. The severe implications resulting from loss of connectivity has resulted in several management actions that target connectivity between river systems and the sea (McKinnell et al., 1994; Lundqvist et al., 2008; Serrano et al., 2009). Knowledge of migration timing has enabled managers to adopt actions that are flexible in time, which may increase their acceptance by impacted stakeholders like the hydroelectric power industry. These have included diverting water from hydroelectric dams to a bypass during the migratory period only, or transporting salmon 88 km upstream in trucks from the first barrier to the spawning grounds (Lundqvist et al., 2008; Serrano et al., 2009; Hagelin et al., 2015).

Meanwhile, a key aim should be to reduce the amount of fishing effort in the Main Basin, due to stock mixing, which includes threatened stocks. Instead, fishing efforts could be focused in coastal areas or river estuaries where the stock status is known. Understanding the movements of hatchery-reared salmon may also identify alternative management actions for implementation. Research indicates that hatchery-reared salmon are more likely to be caught in the Bothnian Sea compared to wild stocks because hatchery-reared salmon are less likely to migrate to the Main Basin of the Baltic Sea (Jutala et al., 2003). Hatchery-reared salmon may also arrive in the northern Baltic later than wild salmon stocks (McKinnell et al., 1994). This knowledge may be used to implement a time-area based approach, providing a potentially viable management option that maintains recreational and commercial harvesting whilst simultaneously increasing the harvest of hatchery-reared salmon.

Step 4—Implementation

The management of salmon influences a number of stakeholders like commercial fisheries, the power industry, general public, and conservation community. Understanding the movement ecology of salmon has enabled managers to identify actions that have a higher likelihood of acceptance by stakeholders and thus improved effectiveness. An example includes the time-area based approach for fisheries, whereby the coastal fishery is opened later in the season meaning that most wild salmon have already entered the river system and the fisheries harvest is dominated by hatchery-reared salmon (ICES, 2012). Such an approach maintains the livelihoods of fisherman whilst reducing harvest pressure on wild salmon and thus achieving conservation targets. Another example is how the knowledge of timing of salmon migrations enables hydroelectric dams to regulate discharge rates, which target conservation goals during the salmon migration and electricity production at other times of the year (Lundqvist et al., 2008; Håkansson, 2009). Achieving management targets increasingly relies upon identifying trade-offs that are acceptable to all stakeholders (Redpath et al., 2013). By linking movement ecology with management, alternative management actions can be identified that allow managers to explore trade-off scenarios with stakeholders, which increase the implementation potential of proposed management actions.

Several management actions for salmon are executed within national boundaries, such as maintaining connectivity in freshwater systems, improving breeding habitats, and managing coastal fisheries. However, during the marine phase of the salmon

life cycle, the nomadic movements of adults need transboundary collaborations for effective management. The Main Basin of the Baltic Sea is an offshore fishery that is exploited by many countries in the region. Therefore, international measures are needed to effectively manage the mixed-stock fishery and knowledge of movements and genetics is vital to achieve this goal. Harvest quotas are provided by the Common Fisheries Policy but the Atlantic salmon would benefit further from the re-establishment of an International Baltic Treaty. Transboundary collaborations provide a number of challenges that influence the implementation potential of management actions (Kark et al., 2015). These may include increased financial costs, delayed conservation planning or countries “free-riding” on the assumption that management actions will be implemented by other countries (Kark et al., 2009, 2015). However, transboundary collaborations may also improve the cost effectiveness of management and increase the scale of management to more effectively manage a highly mobile species (Kark et al., 2015).

Step 5—Evaluation

Mathematical and statistical models have been developed that link biological and economic data to identify management actions for salmon in the Baltic (Kulmala et al., 2008). Kulmala et al. (2008) explicitly incorporate the migratory movements of salmon to determine optimal harvest solutions, and identify that driftnet fisheries should be excluded as a harvest method. Several studies have also evaluated the effectiveness of management plans prior to their implementation, which include both national plans and international plans (Haapasaari and Karjalainen, 2010; Levontin et al., 2011). Bayesian network analyses have been used to incorporate several sources of data that include the biology of the species, expert knowledge, and sociological data to evaluate alternative management options (Haapasaari and Karjalainen, 2010; Levontin et al., 2011). These studies have determined the commitment of stakeholders to management options and how this may influence the effectiveness of proposed management actions (Haapasaari and Karjalainen, 2010; Levontin et al., 2011).

With regards to movement, management interventions like fish ladders may not guarantee connectivity, as illustrated by Lundqvist et al. (2008). The project evaluation found that salmon migrating upstream were not drawn to the bypass containing the fish ladder, due to differing discharge rates from the hydroelectric dam and the bypass. Salmon survival was also reduced the following spring as salmon were not drawn to the fish ladder during the seawards migration, but traveled through the turbines instead. Improved knowledge of the movement ecology of salmon, such as how they move in the river and what cues they are drawn to are needed to improve the designs of existing and future connectivity measures (Lundqvist et al., 2008). In addition, management actions are not being implemented for the full movement cycle. In the example of transporting salmon upstream by truck, no actions are being taken for the downstream migration of salmon, resulting in very low survival rates (Bergman et al., 2014; Hagelin et al., 2015). The recovery of this river's stock is therefore limited by not considering the migratory connectivity of both

upstream and downstream migrations. In this instance it would be important to evaluate both the effectiveness of translocating individuals to spawning areas (Fischer and Lindenmayer, 2000), and subsequently whether the action is meeting management objectives of population recovery.

MANAGEMENT IMPLICATIONS

Studies continue to highlight that management actions focused in one area, such as protected areas, are not sufficient for effectively conserving a species (Thirgood et al., 2004; Martin et al., 2007; Runge et al., 2014). Shortfalls include the scale of management, conflicts with stakeholders, alternative land-uses and limited space available (Sanderson et al., 2002; Runge et al., 2014; Symes et al., 2015). Management actions focused in one area also fail to account for species movements (Thirgood et al., 2004; Runge et al., 2014). Linking movement ecology to conservation has several implications for the future management of wildlife. Understanding a species movements enable managers to implement actions along the entire movement path, such as a flyway approach for birds and butterflies (Klaassen et al., 2008; Howard and Davis, 2009) or dynamic protected areas in the ocean (Shillinger et al., 2008; Game et al., 2009) and on land (Singh and Milner-Gulland, 2011; Bull et al., 2013). Understanding movement also enables managers to identify threats, such as the loss of important sites (Iwamura et al., 2013) or barriers to movement (Seidler et al., 2015), and therefore prioritize the most effective management actions that have the highest chance of success (Game et al., 2013; Auerbach et al., 2014; Tulloch et al., 2015). Knowledge of species movements allows managers to identify alternative management actions that are flexible in space and time, such as time-area based approaches that are used to flood wetlands for migratory waterfowl (O'Neal et al., 2008) or time-restricted harvesting practices (Hunter et al., 2006). Knowing where and when a

species will be is a pre-requisite for the successful implementation of time-area approaches, which allow managers to develop trade-off scenarios that balance conservation needs with alternative land-use practices (O'Neal et al., 2008; Shillinger et al., 2008; Game et al., 2009; Redpath et al., 2013).

We have highlighted how knowledge gained from movement ecology can be used to identify alternative, complementary strategies in wildlife management. Our conceptual framework provides a step by step workflow that aims to understand the movement patterns of a species and use this knowledge to guide management actions. As the field of movement ecology continues to grow, it is important to strengthen the link with wildlife management to further improve the decision-making capabilities of practitioners and managers.

AUTHOR CONTRIBUTIONS

AA and NS conceived the idea. AA wrote the majority of the manuscript with input from NS

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