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Social interactions shape the timing of spawning migrations in an anadromous fish

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Mass migrations are found throughout the animal kingdom and are often undertaken by coordinated social groups. However, surprisingly little is known about how social interactions influence migratory timing. Anadromous fishes such as salmon make extensive breeding migrations between marine and freshwater ecosystems. Returning adult salmon tend to move in discrete temporal pulses, which are typically thought to be triggered by abiotic environmental stimuli (e.g. changes in river flow or temperature). However, most studies reveal only weak correlations between abiotic factors and the timing of spawning runs. Here, we demonstrate that social interactions provide a plausible alternative or additional explanation for such patterns. We first provide an example of the phenomenon using 20 years of data on sockeye salmon, *Oncorhynchus nerka*, ascending a stream in pulses in the absence of any obvious environmental triggers. Next, we present a model that reproduces the pulses observed in the data, simply by including social interactions among individuals. Deviations between the empirical data and the social model results suggest that salmon may alter their individual behaviour in response to annual fluctuations in density. We hope our results, demonstrating the role that social influence can play on migration timing, will motivate further studies exploring how social interactions may shape the movements of other migratory taxa. Understanding how individuals integrate social information with internal and exogenous drivers of migratory behaviour is vital, particularly in the face of a changing climate, which is changing both the cues used for, and the optimal timing of, migrations.

Migration is a widespread phenomenon throughout the animal kingdom, allowing populations to take advantage of temporally predictable foraging and breeding conditions in discrete habitats that cannot be used simultaneously (Dingle, 2014). While availability of resources is likely an ultimate explanation for migration, the timing of when individuals or groups migrate is influenced by various proximate stimuli (McNamara, Barta, Klaassen, & Bauer, 2011). In many taxa, a complex combination of internal physiological rhythms, seasonal changes in photoperiod and localized cues such as temperature, wind or river flow, and other stimuli influence decisions to migrate at a given time (Dingle & Drake, 2007). Coordinated mass movement is exceedingly common in migratory taxa (Milner-Gulland, Fryxell, & Sinclair, 2011). Thus social information likely also influences an individual's decision as to when to migrate. Specifically, individuals preparing for migrations may differ in their internal state of readiness (Nathan et al., 2008) but contact with individuals at a more advanced state of readiness might be sufficient to initiate migration in some animals that might otherwise not commence migrating at that time (Helm, Piersma, & Van der Jeugd, 2006).

Given the ubiquity of social migration, it is surprising that studies of the mechanisms driving migrations are often conducted on animals in isolation (Bingman & Cheng, 2005; Gould & Gould, 2012). Moreover, as discussed by Helm et al. (2006), the role of social collective decisions are most often explored within spatial contexts (i.e. where to go) (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; Dell'Ariccia, Dell'Omo, Wolfer, & Lipp, 2008; Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013), rather than temporal contexts (i.e. when to go) (although see Conradt & Roper, 2000, 2005). Of the work done on social influence on temporal synchronization, most has been done in birds (Helm et al., 2006), where for example, social interactions appear to coordinate waves of sleep and breeding synchrony in bird colonies (Beauchamp,

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2011; Evans, Ardia, & Flux, 2009). More generally, along with birds, fishes and mammals signal to initiate synchronized movement, although not necessarily in a migratory context (Black, 1988; Stewart & Harcourt, 1994; Ward et al., 2013). Here, we address this research gap by taking advantage of an unusually fine-grained, yet long-term, migration data set from anadromous salmon to develop and test a generic model for social influence on migration.

Pacific and Atlantic salmon are well known for their homing migrations back from the ocean to natal sites for reproduction (Jonsson & Jonsson, 2011; Quinn, 2005). As with many other migratory animals, salmon support important commercial, recreational, subsistence and ceremonial fisheries (National Research Council, 1996) and transfer nutrients from the ocean to freshwater environments, where they affect all trophic levels from periphyton (Kline, Goering, Mathisen, Poe, & Parker, 1990) to bears (Hilderbrand, Jenkins, Schwartz, Hanley, & Robbins, 1999) in both terrestrial and aquatic environments (Bilby, Fransen, & Bisson, 1996; Willson & Halupka, 1995). Migration timing is a key uncertainty in the management of salmon fisheries because it can confound perceptions of population size as fish enter a fishery (Adkison, Cunningham, & Jonsson, 2015; Mundy & Evenson, 2011). Therefore, decades of research have been devoted to understanding the broad-scale and fine-scale aspects of salmon migration timing (Banks, 1969).

Most attempts to explain salmon migration timing primarily focus on correlations to abiotic environmental stimuli (Loughlin, Clarke, Pennell, McCarthy, & Sellars, 2016; Neave, 1943). However, in general, the movement of adult salmon in rivers often seems to be independent of any obvious environmental cues, as indicated by the general failure to successfully model migration based on such cues (Lilja & Romakkaniemi, 2003; Trépanier, Rodriguez, & Magnan, 1996). Although, in some cases, increased stream flow is needed for the fish to access upstream habitats (Davidson, Vaughan, & Hutchinson, 1943; Shapovalov & Taft, 1954). When the data on upstream salmon migration are pooled among many years, the timing tends to approximate a smooth normal distribution, but within any given year, salmon tend to move in seemingly unpredictable discrete pulses (Hunter, 1959; Quinn & Myers, 2004; Quinn, McGinnity, & Reed, 2016). Because external cues often do not adequately explain the timing of these discrete pulses, it is likely that other processes shape the commonly observed patterns of timing.

We hypothesize that social interactions may provide a mechanism for the pulsed arrival patterns observed during animal migrations. As a case study, we explore the role of social interactions on the timing of migration movements, using data on a population of wild sockeye salmon, *Oncorhynchus nerka*. We focus on the final phase of the migration as fish are readily quantified in the shallow waters of the breeding stream and because timing of entry into the breeding grounds is under selection and influences individual fitness. Despite an apparent lack of abiotic environmental triggers, the salmon in this system tend to arrive in discrete pulses. We develop a general migration timing model which incorporates social positive feedback caused by individuals copying other individuals' decisions. This model successfully reproduces the timing patterns observed in the salmon data, suggesting that considering the interplay between internal, exogenous and social drivers could be key to understanding patterns of migratory movement.

METHODS

Site Description

Hansen Creek is a 2 km long tributary of Lake Aleknagik in the Wood River Lakes system, southwestern Alaska (for a map, see Carlson & Quinn, 2007). The creek is very shallow and narrow throughout its length, averaging 10 cm deep and 4 m wide during the months of July and August when adult salmon are present (Marriott, 1964). Although the level of the lake varies substantially from year to year, Hansen Creek is very clear and varies very little in flow within and among seasons due to the buffering effect of ponds, springs and flat sub-basin topography (Carlson & Quinn, 2007; Quinn & Buck, 2001), averaging 0.099 m^3/s during the period when salmon arrive (University of Washington Alaska Salmon Program, n.d.). The stream's small size and stable flow regime make it conducive for observing and quantifying adult salmon and for detecting the influences of social behaviour in the absence of other environmental cues for migration. This region of Alaska has characteristically mild and dry summers; heavy rainfall can occur but often little or no rain falls for several weeks, at which time the stream flows gradually diminish yet salmon ascend the streams with very little variation in overall timing among years.

The migration of sockeye salmon into Hansen Creek and the dozens of other streams in the Wood River Lake system (and salmon in general) occurs in several stages. First, the maturing salmon are widely distributed on the North Pacific Ocean and Bering Sea in the spring of the year, and migrate very rapidly (ca. 40–60 km/day) into Bristol Bay, where they progressively segregate into their natal drainage basins (Quinn, 2005). The salmon then ascend large rivers draining these basins in late June and early July; the fish homing to different natal tributaries are thoroughly mixed at this time (Doctor, Hilborn, Rowse, & Quinn, 2010). The salmon from each population then diverge to the mouths of their respective natal streams, congregate in the lake until they complete the process of sexual maturation, then ascend the small streams in late July and early August, spawn, and die within a few weeks. Individual fish are thus in close proximity to members of their own population prior to entering the natal stream, which each fish ascends when some combination of internal (physiological) condition and external stimuli are sufficient.

Spawning Surveys

During 20 spawning seasons (1997–2016) researchers surveyed sockeye salmon, the only Pacific salmon species in the stream, in Hansen Creek nearly every day that adult fish were present during the spawning season. Each survey day, all live and dead salmon were enumerated. After counting, carcasses were removed beyond 5 m of the creek to avoid repeat sampling. On each day the number of salmon estimated to have arrived in the creek was the total observed (live plus dead) minus the number observed alive on the previous day (Fig. 1). The resulting counts provide precise data on the timing of salmon arrival and are similar in form to the data collected in many migratory fish populations based on visual counts that occur at weirs and dams or in rivers, or by hydroacoustic equipment. These spawning ground surveys were approved by the University of Washington Institutional Animal Care and Use Committee (permit number 3142-01) and the Alaska Department of Fish and Game (e.g. annual permit numbers SF2015-132d, SF2014-145d).

Empirical Data Analysis

After accounting for year-to-year variation in the timing of the run, the density of the run averaged over years, and thus the likelihood of a salmon to arrive on any given day, is given by a discrete normal distribution. The mean and standard deviation of this distribution are likely complicated functions of the interplay between internal physiology (e.g. hormones) and environmental cues (e.g. seasonal changes), which have evolved to guide salmon to the breeding grounds over an appropriate interval of the year. Here we