Journal of Theoretical Biology ∎ (∎∎∎∎) ∎∎∎–∎∎∎

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

An agent-based model of dialect evolution in killer whales

Q1 Olga A. Filatova [a,b,*], Patrick J.O. Miller [a]

[a] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY168LB, Scotland, United Kingdom
[b] Department of Vertebrate Zoology, Faculty of Biology, Moscow State University, Moscow 119991, Russia

HIGHLIGHTS

- We test vocal-learning rules on agent-based model of killer whale population.
- Calls changing by random errors led to a graded distribution of the call phenotype.
- Occasional innovation or error proportional to group variance led to discrete calls.
- Tendency to diverge from kin produced gradual divergence of loose call clusters.
- Model output resembled real dialects only when rules were applied in combinations.

ARTICLE INFO

Article history:
Received 10 September 2014
Received in revised form
10 March 2015
Accepted 15 March 2015

Keywords:
Learning
Dialect
Killer whale
Cultural transmission
Cultural evolution

ABSTRACT

The killer whale is one of the few animal species with vocal dialects that arise from socially learned group-specific call repertoires. We describe a new agent-based model of killer whale populations and test a set of vocal-learning rules to assess which mechanisms may lead to the formation of dialect groupings observed in the wild. We tested a null model with genetic transmission and no learning, and ten models with learning rules that differ by template source (mother or matriline), variation type (random errors or innovations) and type of call change (no divergence from kin vs. divergence from kin). The null model without vocal learning did not produce the pattern of group-specific call repertoires we observe in nature. Learning from either mother alone or the entire matriline with calls changing by random errors produced a graded distribution of the call phenotype, without the discrete call types observed in nature. Introducing occasional innovation or random error proportional to matriline variance yielded more or less discrete and stable call types. A tendency to diverge from the calls of related matrilines provided fast divergence of loose call clusters. A pattern resembling the dialect diversity observed in the wild arose only when rules were applied in combinations and similar outputs could arise from different learning rules and their combinations. Our results emphasize the lack of information on quantitative features of wild killer whale dialects and reveal a set of testable questions that can draw insights into the cultural evolution of killer whale dialects.

1. Introduction

Cultural evolution of behavioral traits transmitted via social learning has attracted the attention of researchers since the 1980s, yielding several models of cultural transmission (Cavalli-Sforza and Feldman, Q2 1981; Mundinger, 1980; Lumsden and Wilson, 1981; Boyd and Richerson, 1985). For example, Cavalli-Sforza and Feldman created a mathematical model that described three modes of cultural transmission: vertical (from parents to offspring), horizontal (between animals from the same generation) and oblique (to non-offspring animals from the next generation). This approach distinguishes cultural evolution from genetic evolution, where offspring acquire traits only vertically from parents (at least in vertebrates). Dawkins (1976) suggested a term Q3 "meme" to refer to a unit of cultural evolution, analogous to "gene" in genetic evolution. These attempts to understand and model cultural evolution have revealed that it is driven by forces similar to those found in genetic evolution, though later a variety of cultural propagation mechanisms were suggested that may not have any close biological analog (Claidière et al., 2014; Strimling et al., 2009). Nevertheless, the main forces of cultural evolution are mutations, drift and selection, analogous to those in genetic evolution. Cultural mutations are transformations in meme structure either by random errors or deliberate innovations. The frequency of different memes in populations may vary due to cultural drift if a meme is neutral, or due to cultural selection if memes have differing fitness consequences.

* Corresponding author at: Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY168LB, Scotland.
Tel.: +44 7580484346.
E-mail address: oaf@st-andrews.ac.uk (O.A. Filatova).

http://dx.doi.org/10.1016/j.jtbi.2015.03.020
0022-5193/© 2015 Published by Elsevier Ltd.

Agent-based models of cultural transmission have proven to be a powerful tool to investigate the rules and consequences of social learning. These models provide valuable insights in the processes that can take hundreds to thousands of years to occur in nature and therefore cannot be studied directly. Agent-based models have been used to examine the general patterns of cultural transmission (e.g. Deffuant et al., 2005; McElreath and Henrich, 2007; Rendell et al., 2010) as well as social learning of particular traits (e.g. bird song: Goodfellow and Slater, 1986; Williams and Slater, 1990; Ellers and Slabbekoorn, 2003).

One of the species with a well-described cultural tradition is the killer whale that possesses a complex system of socially learned vocal dialects. Killer whales have a nested social structure based upon matrilineal kinship. The matrilineal unit comprises a female and up to four generations of her offspring of both sexes. After an oldest female dies, the unit splits into new units according to the number of surviving daughters (Ford, 2002). Units that have split recently often travel together and share a set of stereotyped calls (usually referred to as a vocal dialect), forming pods – the second level of killer whale social structure. With time, as social associations between matrilineal units weaken, pods gradually split as well.

Killer whale vocal traditions were first described by Ford (1991) in two resident populations in the waters around Vancouver Island, British Columbia. Ford hypothesized that dialects are the product of social learning and suggested accumulation of random copying errors and innovations as mechanisms of their evolution: neutral errors and innovations accumulate with time as pods grow and split, leading to more similar dialects between pods that share their recent ancestry.

Extensive evidence supports the hypothesis that killer whale stereotyped calls are learnt rather than transmitted genetically. First, calves adopt the call repertoire of their matrilineal unit, though their fathers usually belong to another matrilineal unit, Q12 usually from a different pod (Barrett-Lennard, 2000), and may therefore have a completely different call repertoire. If call repertoires were transmitted genetically, offspring repertoires should be somehow intermediate between mother's and father's, or (in case of complete dominance) be similar to either mother's or father's calls, but in reality calves appear to inherit only the vocal repertoire of their mother's group without any traces of paternal Q4 input (Miller et al., 2004). Two juvenile killer whales displaced from their natal group also showed indications of vocal learning (Foote et al., 2006). Additionally, some studies in captivity suggest that young killer whales are able to imitate calls of their tank Q5 mates, indicating their vocal learning ability. For example, Bain (1986) described a young female captured in Iceland mimicking Q13 the calls of a Canadian female after sharing a tank for several years. Crance et al. (2014) reported that two young males learned new calls and altered their repertoires to match that of an adult male kept in the same tank. Therefore, vocal learning is the most likely explanation of the dialect sharing pattern in wild killer whales.

Ford (1991) suggested that calves learn their repertoires selectively from their mothers and other members of matrilineal group, rather than from all pod members, leading to small-scale differences between matrilines of the same pod. A pattern of gradual change between matrilineal groups was demonstrated quantitatively, leading to the conclusion that pod-specific calling behaviour gradually develops on the matriline level, simultaneously with the gradual social divergence of matrilines (Miller and Bain, 2000).

Ford (1991) suggested that accumulation of random copying errors can only change existing call types, while the formation of new types requires innovation. This idea has never been tested quantitatively, and innovations have not been described in wild killer whale dialects despite more than 40 years of observations. Call structure has proven to be rather stable over time, with only small-scale quantitative differences observed in diachronic studies (Deecke et al., 2000; Wieland et al., 2010). Therefore, it is likely that call evolution is a slow process and innovation events may occur only too rarely to detect them over the available research period of several tens of years.

Killer whales are a highly suitable candidate species to explore patterns of social learning using agent-based models. Sufficient information exists on their demographic processes and social structure (Bigg et al., 1990; Olesiuk et al., 1990; Ford, 2002) to create 'agents' with realistic life-history parameters. While killer whales are thought to learn their calls, it is generally not feasible to experimentally examine the actual learning patterns of these animals in their natural environment. Agent-based modeling provides a basis to examine different hypotheses of call learning mechanisms in this species, and to consider which mechanisms produce outcomes (in terms of repertoires) that are consistent with observations that can be made. In this study we describe a new agent-based model of a killer whale population and test a set of vocal-learning rules to assess which mechanisms of cultural transmission may lead to the formation of dialect groupings as observed in the wild.

2. Methods

2.1. Features of agent-based model

The description of the agent-based model used here follows the protocol recommended by Grimm et al. (2006, 2010). The model was created in MATLAB.

2.1.1. Purpose

The main purpose of the agent-based model was to reveal which mechanisms of vocal learning may lead to the formation of the vocal dialect patterns observed in the wild. We produce computer-agent killer whales using published demographic parameters, and model social interactions between different agents in the model based upon their social structure. Each individual agent has a specific variable, representing its call, which is modified by specified mechanisms of vocal learning. We estimate the output of the model by comparing the call's parameters with dialect patterns observed in the wild.

2.1.2. State variables and scales

State variables of the model are listed in Table 1. The entities in the model were individual killer whales characterized by the following attributes: age, sex, matriline affiliation and call. Time scale was measured in years; one year was the minimum time step.

Parameters characteristic of the model were death probability, birth probability, values of random learning error and deliberate innovation. Age- and sex-dependent death probability was derived from Olesiuk et al. (1990). A negative density dependent birth probability B_{dd} was calculated every year as

$$B_{dd} = B_{max} * (1 - N_{alive}/K),$$

where B_{max} is the maximum possible yearly birth probability for reproductive female, which was assumed to be 0.33 (once in three years) given killer whale gestation period of 16–17 months, and K is a carrying capacity which was set as 150 whales.

Random learning error was represented by a random number taken from a normal distribution with mean = 0 and standard deviation = 0.01 or 0.05. Innovation was represented by a random number taken from a normal distribution with mean = 0 and standard deviation taken from a binomial distribution with probability of success in each trial = 0.1 or 0.2 (as a result, the innovation was a random number taken from normal distribution with mean = 0 and SD = 1 in one or two of 10 trials and zero in other trials). We intentionally scaled innovation to lead to a much greater change in the call than random errors.