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An agent-based model of dialect evolution in killer whales

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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.

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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, 1981; Mundinger, 1980; Lumsden and Wilson, 1985; 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 "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.

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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, 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 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 mates, indicating their vocal learning ability. For example, Bain (1986) described a young female captured in Iceland mimicking 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.

Table 1
State variables of the model.

Domain	Variable	Value
Individual	Serial number	Integer serial number starting from one
	Age	Integer number of years starting from zero at birth
	Sex	Male or female
	Matriline affiliation	Integer matriline index
	Call	Rational number; at the model start assigned as a random number from a normal distribution with mean = 0 and SD = 0.01 or 0.05
Time	Year	Integer number starting from 1
Population	Death probability	Age- and sex-dependent death probability was derived from Olesiuk et al. (1990) (Tables 9, 11 and 12)
	Birth probability	Negative density dependent birth probability was calculated every year as 0.33⁎(1–N_{alive}/150), where N_{alive} is the number of alive animals
Vocal learning	Random learning error	Random number from a normal distribution with mean = 0 and SD = 0.01 or 0.05
	Innovation	In one or two of 10 trials: random number from a normal distribution with mean = 0 and SD = 1; in other nine or eight trials: zero

Table 2
Overview of call learning rules used in the model.

Rule	Template source	Variability source	Type of selection
(a)	Mother and father	None	None
(b)	Mother	Random learning error	No divergence from the kin
(c)	Matriline		
(d)	Mother	Random learning error plus innovation	
(e)	Matriline		
(h)	Matriline	Random learning error proportional to matriline variance	
(f)	Mother	Random learning error	Divergence from the kin
(g)	Matriline		
(i)	Matriline	Random learning error proportional to matriline variance	
(j)	Mother	Random learning error plus innovation	
(k)	Matriline		

2.1.3. *Process overview and scheduling*

Each model run started by initializing 50 females from 5 different matrilines (10 females per matriline). Each female was 15 years old at the start of the time-course of the model. For these first 50 females, one random call per female was assigned. The call was represented by a random number taken from a normal distribution with mean = 0 and SD = 0.01 or 0.05 (the same as the random learning error).

After initializing females and assigning calls, the model started iterating through the years. Every year, each animal could die with an age- and sex-dependent probability of death derived from Olesiuk et al. (1990). If any animal agent was a female between 15 and 40 years, it could produce an offspring based upon the birth probability for that year. There was 50:50 probability for the newborn agent to be a male or female. Agents aged under 15 years learned their calls every year following specified call learning rules (see below). Call learning was limited to the agents under 15 years because observations suggest that young animals can significantly modify their calls, while the repertoire of adults is more stable (see Bain, 1986; Foote et al., 2006; Crance et al., 2014).

2.1.4. *Design concepts*

2.1.4.1. Collectives. The social structure within the model aimed to mimic social structure described for the resident killer whales in coastal waters of the North Pacific (Bigg et al., 1990; Ivkovich et al., 2010; Matkin et al., 2014): all descendants of a surviving female were considered a single matriline. After the model finished iterating through the animals every year, matrilines were updated to account for the oldest-surviving females that have died during the given year. Every daughter of a just-deceased oldest female became a founder of her own matriline; she and all her offspring were assigned a new matriline number. Sons of just-dead females did not change their matriline number and retained the matriline number of their dead mother for the rest of their lives.

2.1.4.2. Stochasticity. The following processes were modeled by assuming they were random: assignment of call to each agent at the start of the model, birth/death of each agent every year (agent gave birth or died if the random probability was higher than birth probability for this year or death probability for its age/sex class), assignment of sex to the newborn agent, and call learning through adding/subtracting the random learning error.

2.1.4.3. Learning. Each agent aged under 15 years changed its call yearly according to a set of specific rules. The goal of the research was to explore emergent features of the model based upon different learning mechanisms. We explored outcomes of the following learning rules that combined two types of cultural mutations (random errors and innovations), and two types of cultural selection (averaging calls towards matriline template and diverging calls from other matrilines) (for the summary see Table 2):

(a) Null model with no learning, accounting only for genetic inheritance. Calls were passed from mother and father as two discrete alleles. Offspring phenotype (call) was intermediate between mother's and father's alleles. Alleles passed to the next generation unaltered with 50% probability for either of the alleles to be passed to every offspring.
(b) Learning from mother only plus random errors. The learner's call phenotype was calculated by adding a random learning error (see “State variables and scales” for parameters) to the mother's call phenotype.

(c) Learning from the entire matriline plus random errors. The learner's call was calculated by averaging calls from all alive members of its matriline and adding the random learning error.

(d) Learning from mother plus innovations. This learning rule was similar to (b), but occasional innovation was added (see “State variables and scales” for parameters). Random learning error was also retained in this model to provide low-level variability.

(e) Learning from matriline plus innovations. This learning rule was similar to (c), but occasional innovation was added. Random learning error was also retained in this model to provide low-level variability.

(f) Learning from mother plus tendency to diverge from kin. In this model the call template derived from mother was altered during learning to diverge from the calls of related agents. For this, a kinship matrix was calculated based upon the number of common maternal ancestors between the learner agent and all other alive whales (except those from its own matriline). Then, the anti-template call was calculated by averaging calls of all alive whales weighted by their kinship to the learner (so, the calls of closely related agents contributed the most to the anti-template call, and non-related agents from other ancestral lineages did not contribute at all). At the next stage, the learner agent altered the template derived from mother to diverge from the anti-template. This was achieved by adding the absolute value of random learning error if the anti-template call was lower than the mother's template, or subtracting the absolute value of random learning error if otherwise.

(g) Learning from matriline plus tendency to diverge from kin. This model was equal to (f), but the template was obtained by averaging calls from the entire matriline, instead of deriving it from mother only, as in (f).

(h) Learning from matriline plus random error proportional to the variance within the matriline. The learner's call was calculated by averaging calls from members of its matriline and adding the random learning error with standard deviation equal to the standard deviation of the parameter distribution within the matriline. If there was only one whale in the matriline and standard deviation was therefore equal to zero, the usual random error was added instead.

(i) Learning from matriline plus tendency to diverge from kin through the error proportional to the variance within the matriline. This learning rule was a combination of (g) and (h). The process was the same as (g), but the learning error had a standard deviation equal to that of the entire matriline's call phenotype.

(j) Model (f) plus innovations. This learning rule was a combination of (d) and (f). The process was the same as (f), but at the last stage we added the occasional innovation.

(k) Model (g) plus innovations. This learning rule was a combination of (e) and (g). The process was the same as (g), but at the last stage we added the occasional innovation.

2.1.4.4. Emergence. Emergent properties from the agent-based model were: the speed of call change, the level of divergence of calls across matrilines and discreteness of different branches of an evolutionary tree. We compared the emergent properties of the model to properties of the real dialects in nature to evaluate the likelihood of each learning rule. There are few studies examining evolutionary patterns in wild killer whale dialects, because the correct study design requires long time series of recordings from known matrilines. None of these studies report quantitative parameters of inter- and intra-matriline similarity suitable to compare with output of our model, so we evaluated the model results qualitatively rather than quantitatively. Basically, we expected the following outcomes: calls diverging as discrete branches of an evolutionary tree (Ford, 1991), more similar within than between matrilines (Nousek et al., 2006), evolving quickly enough to accumulate the detectable changes over the span of several tens of years (Deecke et al., 2000).

As an emergent property of each model run, we calculated the similarity of calls across matrilines, the speed of call change and the level of bimodality of the resulting call phenotype distribution, and produced a graphical representation of the resulting call phenotype distribution. The similarity of calls across matrilines (matriline similarity, *MS*) was calculated as mean variance within matrilines divided by mean total variance of calls of all whales that were alive at the end of evolution:

$$MS = \frac{(1/m) * \sum_{i=1}^{m} Var_i}{Var_{all}}$$

where m is the number of matrilines with >1 alive agents by the end of the evolution, Var_i is the variance within each matriline, Var_{all} is the total variance among all alive animals. This parameter was negatively related to the degree of matriline divergence from each other, so we expected it to be lower in models that more effectively yielded matriline divergence.

The speed of call change (SCC) was calculated as sum of squares of call values divided by years and number of alive animals at the end of evolution, and multiplied by 100 as a scalar:

$$SCC = \frac{100}{yrs * n} \sum_{j=1}^{n} C_j^2$$

where yrs is the number of years of evolution (500 in our models), n is the number of agents alive by the end of the evolution, and C_j is a call value of each agent.

The level of bimodality reflected the discreteness of branches in the resulting call phenotype distribution. It was calculated through Hartigan's dip test of unimodality (Hartigan and Hartigan, 1985) using hartigansdiptest.m function (http://www.nicprice.net/diptest/). If the output of this function is more than about 0.05, it indicates that the distribution is not unimodal, i.e. it has relatively discrete branches.

These numerical values were used to compare the models with different types of learning, while the general decision of the model likelihood was based upon the graphical representation of the model output.

3. Results

The null model with simple genetic transmission of calls and no learning did not yield any call change with time, but the variability of calls reduced with time because many alleles died out, and only few remained in the population.

Graphical outputs of the models with random error $SD=0.01$ and probability of innovation$=0.1$ after 500 model years are shown in Fig. 1. When the calls were changed with time only by random error (learning rules (b) and (c)), divergence between matrilines occurred to some extent, but the distribution of the call phenotype became graded, without discrete call types observed in wild killer whales (Fig. 1b and c). When learning from the entire matriline, some branches occasionally separated from the continuum but later joined again because the random error altered the matriline template. Matriline divergence and bimodality were higher when the call template was averaged from all matriline members than when it was obtained from mother (Fig. 2).

When calls changed via occasional innovations (learning rules (d) and (e)), more or less discrete call types formed in punctuated steps (Fig. 1d and e). When learning from mother, call types were discrete and rather stable through the years; call divergence occurred only through formation of new discrete calls and loss of old ones. When learning from the entire matriline, types were

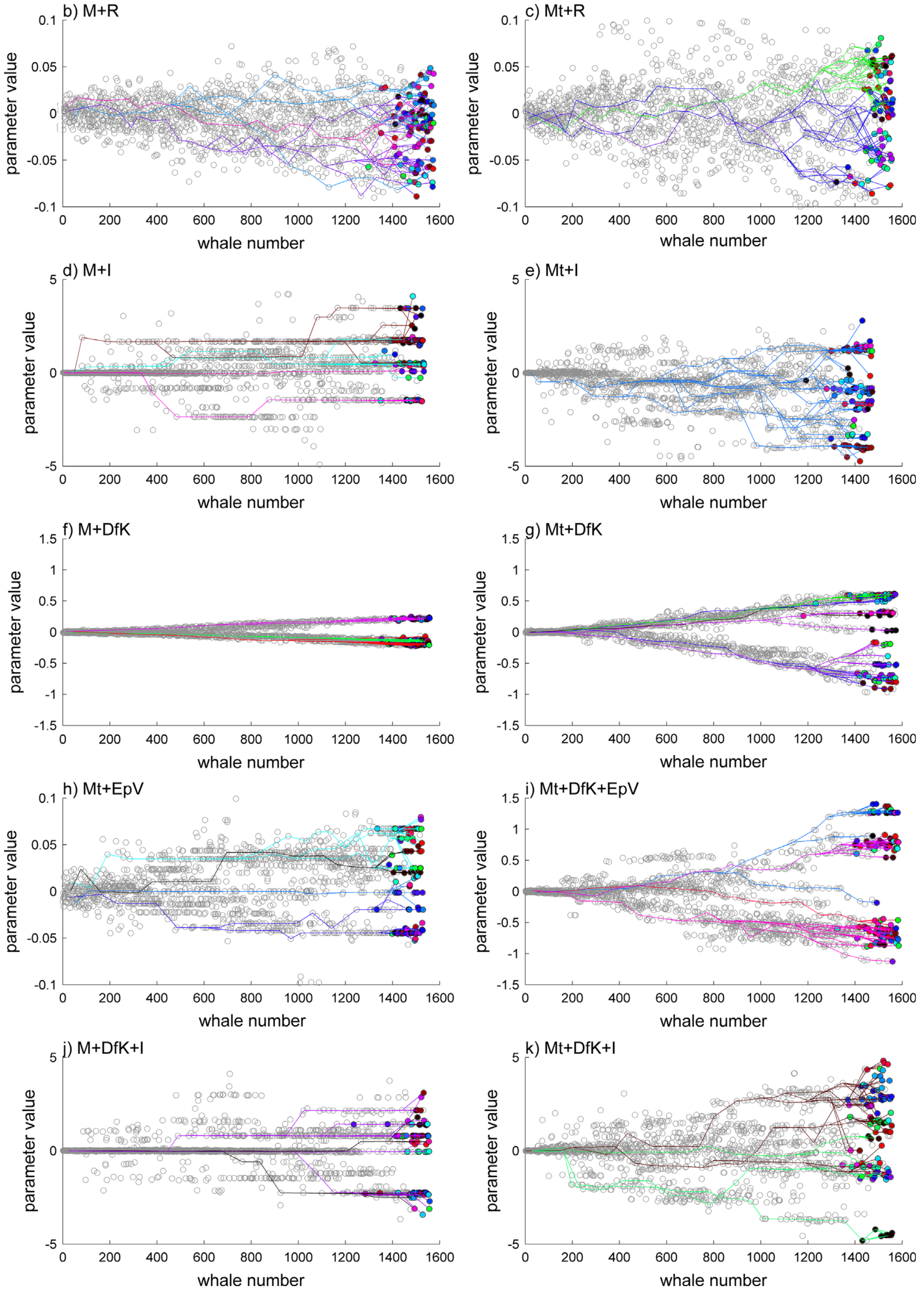

Fig. 1. Results of modeling with random error SD=0.01 and probability of innovation=0.1. Each graph shows all animals in gray and the animals alive by the end of evolution in color. Color reflects matriline membership (members of the same matriline have the same color). Lines show the ancestors of alive whales, line color indicates the first ancestor. Note different *y*-axis scales: −0.1 to 0.1 in models with random error, −1.5 to 1.5 in models with divergence from kin and −5 to 5 in models with innovations. Letters (b)–(k) correspond to the model indices in the text and Table 2. Abbreviations describe the model: M – learning from mother, Mt – learning from matriline, R – call change through random errors, I – call change through innovations, DfK – divergence from the kin, EpV – error proportional to variance in the matriline. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

less stable and less discrete. The divergence between matrilines was higher, but bimodality was lower when learning from matriline compared with learning from mother. The total level of matriline divergence was similar to that when calls changed through random errors only, but the speed of call change was about 1000 times faster (Fig. 2).

When calls were learned with tendency to diverge by random learning error from the calls of the related whales proportional to kinship (closer kinship increased the tendency to diverge – learning rules (f) and (g)), calls diverged gradually with time forming loose clusters (Fig. 1f and g). Usually two constantly diverging clusters formed, which could include calls from different ancestral lineages. Divergence between matrilines was ten times higher and speed of call change was about 20 times faster when learning from the whole matriline vs. learning only from mother, while bimodality was similar in both cases.

When calls changed by error proportional to the variance within learner agent's matriline (learning rule (h)), loose call clusters formed (Fig.1h); the pattern and bimodality were intermediate between those observed during learning from mother and from matriline with call change via innovation (models (d) and (e)), but divergence between matrilines was higher than in both of these models (Fig. 2).

When calls were learned with tendency to diverge from calls of the related whales by error proportional to the variance within learner agent's matriline (learning rule (i)), it produced loose gradually diverging clusters (Fig. 1i). The pattern was generally similar to call change through divergence from kin, but usually yielded more than two branches (Fig. 2).

When calls were changed by tendency to diverge from the kin plus occasional innovations (learning rules (j) and (k)), discrete calls formed in punctuated steps. When learning from mother, call types were more discrete and stable than when learning from matriline. The pattern and the emergent properties were generally similar to the learning through innovation only (Figs. 1j, k and 2).

Setting the standard deviation of random learning error to 0.05 instead of 0.01 did not change the outcome of the models where the random error was the only mode of call change ((b)–(c), (f)–(i)) apart from increasing the speed of call change. In the models with innovations ((d),(e)) increasing the random error yielded looser clusters (Fig. 3d and e). In the models with innovations and divergence from kin ((j),(k)) increasing the random error led to gradual divergence of the discrete call types (Fig. 2j and k).

Setting the probability of innovation to 0.2 instead of 0.1 yielded looser clusters in all models that involved innovations ((d), (e), (j), (k)) (Fig. 4).

4. Discussion

Agent-based modeling showed that a simple call phenotype-acquisition processes not involving vocal learning modeled here could not produce the pattern of group-specific call repertoires we observe in nature. Learning from either mother alone or the entire matriline with a change of calls by random errors resulted in graded distribution of the call phenotype parameters across the population instead of forming the discrete call types observed in the wild. Some divergence between matrilines was achieved, but the calls of agents from different matrilies were often more similar than the calls of agents from the same matriline, contrary to what was reported in the wild killer whales (Nousek et al., 2006).

Ford (1991) hypothesized that random errors can only alter the existing call types, while the formation of new types requires innovation. Indeed, when occasional innovation was introduced into the model, discrete call types did form. Setting a higher probability of innovation yielded looser clusters, suggesting that

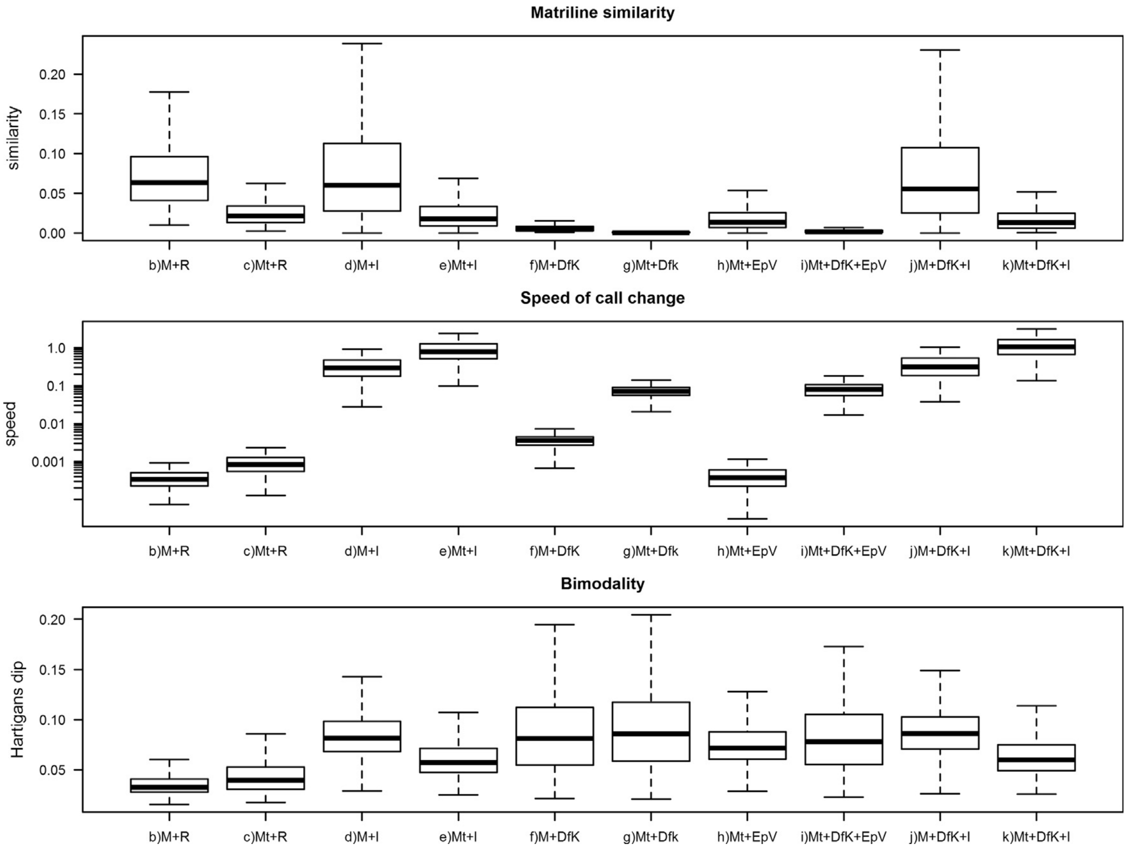

Fig. 2. Emergent properties after 500 model years. Note the logarithmic *y*-axis on the middle graph.

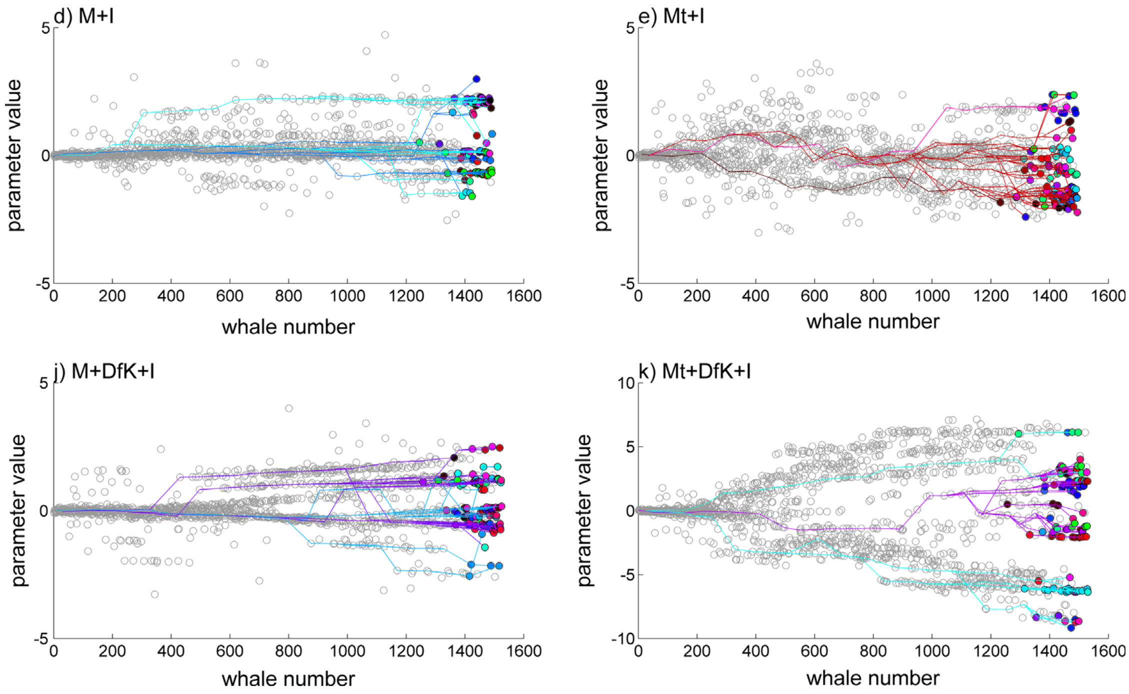

Fig. 3. Results of modeling with random error SD=0.05 and probability of innovation=0.1. Note different *y*-axis scales: −5 to 5 on the first three plots and −10 to 10 on the last plot. Legend is the same as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

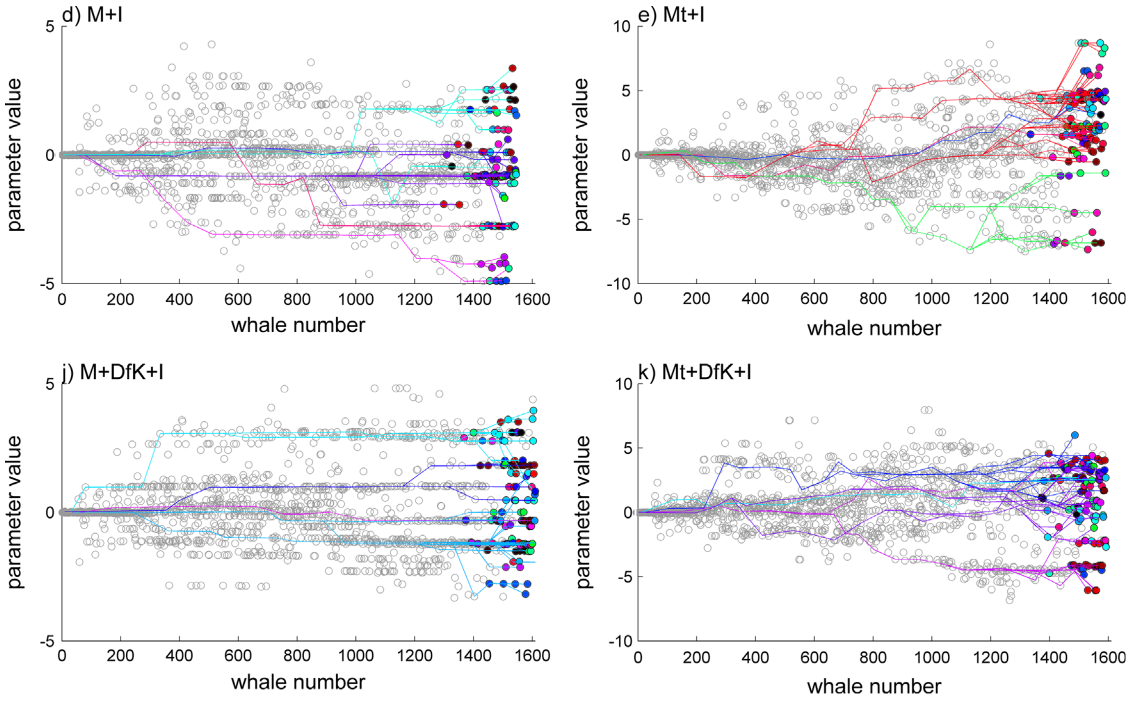

Fig. 4. Results of modeling with random error SD=0.01 and probability of innovation=0.2. Note different *y*-axis scales: −5 to 5 on the left plots and −10 to 10 on the right plots. Legend is the same as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

innovation should be rare to produce discrete types. When agents learnt only from their mothers, calls were relatively stable in time without any divergence; when agents learnt from the entire matriline, calls were less stable and less discrete.

There is no empirical evidence for the gradual divergence of call types in wild killer whales, and it is possible that new call types form only through occasional innovations. So, the occasional innovation combined with random errors is sufficient to produce the repertoires of discrete call types observed in nature, but some other mechanism is likely to be responsible for the divergence of the shared call types in related matrilines, because in the dialects of the wild killer whales divergence between groups is too high to be explained by random errors, but too gradual to form through innovations (Miller and Bain, 2000). We tested two possible mechanisms in our model: the tendency to diverge from calls of related matrilines by random error and call change by error proportional to the variance within learner agent's matriline.

The tendency to diverge from calls of related matrilines by random error produced gradual divergence of loose call clusters. Within the clusters, the distribution of call parameter was rather gradual; some matriline divergence was observed, but many matrilines still overlapped.

Grebner et al. (2011) suggested that new stereotyped calls in killer whale repertoires may arise from the gradual modification of existing call types through subtypes. They reported the formation of four distinct subtypes in a call type that had been previously described as a single subtype with graded variability (Ford, 1987). According to our model, such a process cannot be a result of random errors. We modeled a possible scenario of this process by setting the value for learning error to be proportional to the total variance in the learner agent's matriline. This yielded some matriline divergence and occasional formation of discrete clusters, suggesting that this process may play a role in dialect evolution. Interestingly, the output of this model resembled those of the model with innovations, indicating that similar patterns may arise from completely different learning rules.

Therefore, it appears that both innovation and crystallizing the types from the continuum can be possible sources of discrete calls, and divergence of shared calls in related matrilines can be achieved to some extent by the tendency to diverge from kin. Our last two models combined these processes.

Tendency to diverge from kin by error proportional to the variance within learner agent's matriline produced diverging clusters that were more discrete than when changing calls only through divergence from kin, but less discrete than when changing through innovations. Innovations combined with divergence from kin led to discrete call types evolving in punctuated steps and diverging on smaller scale across matrilines when random error SD was 0.01. However, when SD of the random error was set at 0.05 instead of 0.01 (Fig. 2j and k), the output of this model yielded the diverging clusters similar to those produced by tendency to diverge from kin by error proportional to the matriline variance, confirming that different learning rules can produce similar patterns.

These models combining two learning rules appear to yield a phenotype pattern most similar to that observed in nature for resident killer whales. It combines long-term stability of general call structure with slow gradual change of some parameters. The stability of call structure has been observed in the wild through studies dating back up to 40 years: the general structure of stereotyped calls in recent recordings (e.g. Wieland et al., 2010) corresponds to that from the recordings made in 1970–1990 (Ford, 1987). Also these models resulted in small-scale changes of phenotype parameters in some calls and stability of the others. In the wild, quantitative analysis demonstrated small changes in parameters of some calls over years, while other call parameters were constant, which corresponds to the predictions of this model. For example, Deecke et al. (2000) described the directional change over 12-year period in one of the two studied call types, but not in the other. Wieland et al. (2010) showed differences in duration of some call types over the period of 28 years, but duration of other call types did not change significantly over this period. Filatova et al. (2013) proposed variable speed of change of different call parameters based on the contemporary patterns of call similarity across matrilines.

The formation of new call types through punctuated steps is analogous to the theory of punctuated equilibrium (Eldredge and Gould, 1972), which proposed that biological evolution occurs through rare events of rapid change, separated by extended stationary periods (Gould and Eldredge, 1977), in contrast to the traditional theory of gradual evolutionary changes. The evolution of human languages through punctuational bursts was demonstrated by Atkinson et al. (2008) using quantitative phylogenetic methods.

The tendency to diverge from calls of related matrilines was an important feature of our model that allowed divergence between matrilines over time. The tendency to diverge from similar sounds was shown to be a driving factor in the evolution of other learned signal systems. For example, Nordby et al. (2007) demonstrated that young song sparrows (*Melospiza melodia*) often modified their songs to make them less similar to the songs of their neighbors. Labov (2011) suggested the tendency to maximize variability inside the system as one of the global factors in the evolution of human languages. In cetaceans, it was observed that female (but not male) bottlenose dolphin (*Tursiops* sp.) calves developed signature whistles different from those of their mothers (Sayigh et al., 1990).

The tendency to diverge is rare compared to the opposite tendency to converge sounds to those of neighbors/group members, though they may operate in combination. In the examples mentioned above, young song sparrows usually retained song types that were shared with most of their neighbors (Nordby et al., 2007), humans mimicked phonetic changes from other people (Labov, 2011), and whistles became more similar in male bottlenose dolphins that formed stable alliances (Smolker and Pepper, 1999; Watwood et al., 2004). Another example is humpback whale song that remains uniform in all males from the same breeding ground, but constantly changes through the years, which is likely achieved through divergence–convergence mechanisms: whales create innovations in their song to differ from other males, but copy the innovations from the songs of others (Payne et al., 1983; Payne and Payne, 1985).

It appears that convergence and divergence operating on different scales could be a common mechanism of change of learned acoustic repertoires. This process seems analogous to Turing patterns that form through the simple interaction of activator and inhibitor agents in hypothetical animal tissue (Kondo and Miura, 2010). If the diffusion rate of inhibitor is much larger than that of the activator, the random initial fluctuations in the concentration of the activator are enhanced producing stable self-regulatory patters. When divergence in vocal learning operates on a larger geographical or social scale than convergence, a similar process could lead to the emergence of animal groups with different repertoires in the absence of geographical and social boundaries.

In our model the divergence–convergence mechanism operated on different levels of social structure – divergence occurred on the between-matriline level, and convergence – on within-matriline level through averaging matriline calls. However, it is possible that convergence might occur across matrilines depending upon their level of social affiliation. Indeed, there is some evidence in wild killer whales that convergence can operate on the levels of social structure above matriline: Deecke et al. (2000) showed that one of the two studied call types changed in a similar manner over 12-year period in two closely-related matrilines that were part of the same pod. More observations comparing the repertoires of closely-related matrilines of killer whales would be helpful to specify more clearly the social levels at which convergence might occur.

Convergence in animal sounds often appears to occur without the compensating tendency to diverge. Many songbird species have been shown to match their song types to those of their neighbors (e.g. Nelson, 1992). Pups of some bat species exhibited a group signature in isolation calls that became more prominent during ontogeny (Boughman, 1998; Knörnschild et al., 2012). Convergence of call parameters was also shown in pygmy marmosets (*Cebuella pygmaea*; Snowdon and Elowson, 1999), cotton-top tamarins (*Saguinus oedipus*; Weiss et al., 2001) and chimpanzees (*Pan troglodytes*) (Mitani and Gros-Louis, 1998).

The relative rareness of deliberate divergence in animal sounds may reflect the true occurrence of this process in nature as well as observers' ability to detect it. The reason for its rareness may be the fact that sharing signals with neighbors is advantageous in most cases (Lachlan et al. 2004), while divergence is adaptive only in specific circumstances (signature whistles of bottlenose dolphins, Sayigh et al., 1990). In killer whales, the adaptiveness of call divergence is due to the ability of group-specific call repertoires to act as a marker of kinship and social affiliation (Nousek et al., 2006). This marker would provide benefits for social cohesion among mobile groups (Ford, 1991). Another benefit may arise due to sexual selection. It has been suggested that females choose mates with the most dissimilar dialects, which helps to reduce inbreeding (Barrett-Lennard, 2000). This mechanism could favor call evolution towards faster divergence from similar calls.

Another reason why deliberate divergence is rarely reported in animal sounds may be that the human brain has a predisposition to detect similarities, while the differences are intuitively considered less important and often viewed as an intrinsic natural phenomenon. The value of models is that they are (more or less) free from human attitudes, which allows us to identify simple but important patterns that might otherwise be undetected.

The most significant difference between all model outputs and the patterns reported from the wild was that in the models the calls from the same matriline were often more diverse than the calls from different matrilines. It appears logical because the call change has to occur at some point, but it contradicts the reported features of the dialects of wild killer whales (Nousek et al., 2006). The only way to avoid the significant difference between matriline members is to perform the parallel call change in the whole matriline immediately after the matriline splitting event (i.e. when matriarch dies). This prediction is possible to test in the wild killer whales, and could provide significant insights into the dialect evolution processes.

In our model we consider only one call parameter, but many calls have complex structure, consisting of syllables that can appear in different combinations (Yurk, 2005; Shapiro et al., 2011) and may evolve independently of each other (Filatova et al., 2013). Miller and Bain (2000) showed the gradual difference in the same calls of related matrilines, but the level of divergence varied across call parameters. The most distinctive parameter was the terminal component duration which was quite discrete across matrilines, while other parameters were more or less gradual. It is possible that different learning modes work for different syllables to achieve different kinship-resolution levels as well as individual identification. More data on the distribution of the different call parameters in wild killer whales is needed to verify and calibrate patterns revealed by our model.

In conclusion, in this paper we test different learning rules and discuss their likelihood based on the known properties of natural dialects. Our model provides better understanding of the processes of cultural evolution responsible for the formation of killer whale repertoires, raises new questions and identifies priorities for future research. We show that random error is not sufficient to produce repertoires of discrete calls observed in the wild killer whales. It appears that occasional innovation and crystallization of discrete calls from graded continuum are the most likely factors that form discrete calls. The divergence of the shared calls in related matrilines can be achieved by the tendency to diverge from kin. It is important that neither of these processes worked effectively on their own – the picture similar to the observed dialect diversity arose only when they were applied in combinations. One of the most interesting results of our modeling is that similar outputs may arise from different learning rules.

Our results emphasize the lack of information on the features of wild killer whale dialects and depict a set of testable questions that can draw insights into the dialect evolution. Diachronic longitudinal studies may address the question if call change is gradual or punctuated, how fast do calls change and whether it occurs in one whale or in the whole matriline simultaneously. Synchronic studies may compare the level of matriline divergence and the possible variation within matrilines. The results of these studies can confirm or reject the involvement of the processes explored here into the cultural evolution of killer whale dialects.

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