Volume 245 Issue 2 21 March 2007 ISSN 0022-5193

ELSEVIER

Journal of Theoretical Biology

Available online at www.sciencedirect.com
ScienceDirect
Journal of Theoretical Biology 245 (2007) 341–350
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

Learning, climate and the evolution of cultural capacity

Hal Whitehead*

Department of Biology, Dalhousie University, 1355 Oxford St, Halifax, Nova Scotia, Canada B3H 4J1

Received 21 July 2006; received in revised form 2 September 2006; accepted 2 October 2006
Available online 11 October 2006

Abstract

Patterns of environmental variation influence the utility, and thus evolution, of different learning strategies. I use stochastic, individual-based evolutionary models to assess the relative advantages of 15 different learning strategies (genetic determination, individual learning, vertical social learning, horizontal/oblique social learning, and contingent combinations of these) when competing in variable environments described by 1/f noise. When environmental variation has little effect on fitness, then genetic determinism persists. When environmental variation is large and equal over all time-scales (“white noise”) then individual learning is adaptive. Social learning is advantageous in “red noise” environments when variation over long time-scales is large. Climatic variability increases with time-scale, so that short-lived organisms should be able to rely largely on genetic determination. Thermal climates usually are insufficiently red for social learning to be advantageous for species whose fitness is very determined by temperature. In contrast, population trajectories of many species, especially large mammals and aquatic carnivores, are sufficiently red to promote social learning in their predators. The ocean environment is generally redder than that on land. Thus, while individual learning should be adaptive for many longer-lived organisms, social learning will often be found in those dependent on the populations of other species, especially if they are marine. This provides a potential explanation for the evolution of a prevalence of social learning, and culture, in humans and cetaceans.

Keywords: Learning; Climate; Evolution; 1/f noise

1. Introduction

Behavior may be determined in several ways. These include direct genetic determination, individual learning and social learning, as well as combinations of these. Social learning can be from parents (vertical), other models of the previous generation (oblique), or peers (horizontal). Each of these learning tactics has benefits and costs. In any environment a particular type of behavior will be optimal, and the further removed actual behavior is from this optimal type, the lower the expected fitness of the organism. Individual learning—in which the organism experimentally adjusts its behavior—will usually track a varying environment most closely but may be costly in terms of time, energy, predation risk, and the metabolic costs required to operate an efficient learning control system (such as a brain). Social learning—in which the behavior of other organisms is copied or learned as a consequence of sociality—will be usually less costly and may produce efficient behavior, although perhaps not in some environments. Cheapest of all is direct genetic determinism of behavior, but this may lead to severely suboptimal behavior in variable environments. These trade-offs imply that ecology was a major driver of the evolution of learning (Lefebvre and Palmeta, 1988).

Following this reasoning, several authors have suggested, and illustrated using a variety of verbal and analytical models, that patterns of environmental variation should affect the evolution of different modes of behavioral control (Boyd and Richerson, 1983, 1985, 1988, 1996; Feldman et al., 1996; Lachmann and Jablonka, 1996; Laland et al., 1996; Wakano et al., 2004; Aoki et al., 2005). There is particular interest in the evolution of social learning, as social learning is the basis of culture, and cultural evolution can move behavior and population biology into radical paths, as shown dramatically in the case of modern humans (Richerson and Boyd, 2004).

---

*Tel.: +1 902 494 3723; fax: +1 902 494 3736.
E-mail address: hwhitehe@dal.ca.

0022-5193/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2006.10.001

Richerson and Boyd (1998, 2004) have suggested that advanced cultural capacity and rapid cultural evolution in humans originated in the Pleistocene when environmental variation was high. Similarly, in trying to explain the apparent prevalence of cultural capacity in the cetaceans (whales and dolphins), Rendell and Whitehead (2001) noted that patterns of environmental variation in the ocean are "redder" (i.e. have proportionally greater variance over longer time periods) than on land (Steele, 1985), and that this might promote social learning.

The models behind these suggestions make many simplifying assumptions of necessity. In the analytical models, only two or three (in the cases of Wakano et al., 2004; Aoki et al., 2005) learning strategies are compared, and environmental variation is described by a two-state Markov model (e.g. Boyd and Richerson, 1988; Lachmann and Jablonka, 1996) or first-order autoregressive model (e.g. Boyd and Richerson, 1985), whereas real environmental variation is complex, and includes elements of many frequencies whose significance may vary with habitat and time period (Steele, 1985). Despite these simplifications, analytical models of the evolution of learning in variable environments quickly lose tractability, requiring simplifying assumptions and making results uncertain (Aoki, 1991). Therefore, when analysing the evolution of learning strategies, there has been a recent move towards simulation modeling. When considering the effects of environmental variation, Aoki et al. (2005) used randomization to select between analytical models of constant and changed environments.

Here, I simulate environmental variation with a range of characteristics using the 1/f noise family of models, described by the slope of the inverse of the power frequency spectrum (ω), and an amplitude measured by the standard deviation of the noise as a proportion of the standard deviation of a Gaussian fitness-environment function. 1/f models provide a good description of environmental fluctuation, having considerable empirical support (Halley, 1996), and being used in many ecological and evolutionary models (Gisiger, 2001). I examine the evolution of behavioral control strategies in different 1/f environments using individually based evolutionary stochastic models for populations with both semelparous (in which each individual has only one birth interval, and so generations do not overlap) and iteroparous (in which individuals may give birth in several intervals, so generations overlap) breeding. Unlike previous models, this approach allows 15 learning strategies to compete simultaneously against one another in complex environments. The primary learning tactics, in order of increasing cost, are genetic determination, vertical (parental) social learning, oblique/horizontal (from the general population) social learning, and individual learning. Contingent strategies include combinations of these, in which, at any time, individuals adopt that tactic with the greatest expected fitness, but pay an additional cost for the ability to choose. The principal goal of the analysis is to predict the learning strategies that are likely to evolve in different environmental conditions.

2. Methods

The models consider a univariate environment with value y(t) at time t. Individuals have behavior expressed by a univariate measure x(i,t), the behavior of individual i at time t. The fitness of individual i at time t is given by the Gaussian function (as in Boyd and Richerson, 1985):

$$w(i,t) = D(i)C_{u(i,t)}e^{|x(i,t)-y(t)|^2/2q^2}. \tag{1}$$

Thus the closer x(i,t) is to y(t), the better its behavior tracks the environment, and the more successful the animal. q is the SD of the fitness function, such that a small q gives large penalties for failing to track the environment closely. Without loss of generality, I set $q = 0.8494$ so that if x(i,t) is one unit from y(t) there is a 50% drop in fitness. u(i,t) is a categorical variable indicating he learning tactic used by organism i at time t: either genetic determination ($u = G$), vertical social learning ($u = V$), oblique/horizontal social learning ($u = H$) or individual learning ($u = I$). $C_{u(i,t)}$ reflects the cost of that learning tactic, and D(i) the costs of flexibility, or contingency, in the learning tactics available to individual i. x(i, t) is made up of a target value of the behavior at time t (from genes or learning), X(i,t,u(i,t)), plus some normal random error with mean zero and standard deviation σ, the behavioral accuracy.

Genetically driven behavior ($u = G$) has low baseline cost ($C_G = 1$), and the target behavior is passed accurately from generation to generation, so $X(i,t,G) = X(P(i),t_b(i),G)$ (where P(i) is the parent of i, and $t_b(i)$ is the time unit of birth for i), and the realized behavior varies around this. Somewhat more costly because of the energy and time needed to develop the physiology for social learning, and to learn, is social learning in which realized behavior of other individuals in previous time units becomes the target behavior. Social learning comes in two possible forms: vertical ($u = V$) where learning is from the parent only so the realized behavior of the parent becomes the target behavior of the offspring, $X(i,t,V) = x(P(i),t_b(i))$ and oblique/horizontal ($u = H$), where the mean realized behavior of all individuals in the previous time unit is used as the target behavior, $X(i,t,H) = \text{Mean}[x(j,t-1)]$. Vertical social learning is assumed to be less costly than oblique/horizontal ($C_H < C_V < 1$) as the behavior of fewer models is observed. Individual learning ($u = I$), in which the target behavior is that which maximizes fitness, $X(i,t,I) = y(t)$, is most accurate and costly ($C_I < C_H$). The ordering of these costs is consistent with that in previous models (e.g. Boyd and Richerson, 1985). Changing this ordering will radically change the results of the modelling.

Some individuals are restricted to one of the four tactics, so their learning strategy is either genetic determination, vertical social learning, oblique/horizontal social learning or individual learning. Others have contingent strategies, in which two or more of the basic tactics are considered at each time unit, and the individual adopts the one with maximum expected fitness. The expected fitness for individual i at time t adopting tactic u is given by

$$\mathbf{E}(w(i,t)|u) = \frac{qC_u}{\sigma^2 + q^2}\mathbf{e}^{-(X(i,t,u)-y(t))^2/2(\sigma^2+q^2)} \tag{2}$$

[obtained by integration using Eq. (1) and $x(i,t) = N(X(i,t,u),\sigma)$]. Then the contingent individual adopts that tactic, among those within its contingent set, which maximizes this expectation. This formulation assumes that evolution has led to the adoption of adaptive choice among the basic tactics, but does not assume any particular method for making this choice. All 11 contingent strategies, containing from all 2–4 combinations of the four primary tactics, have some biological plausibility. I assume that possessing the ability of adopting contingent strategies introduces further costs, reducing fitness by a factor of d (<1) if two tactics are available (so $D = d$), $D = d^2$ if three are, and $D = d^3$ for an individual with all four options, whereas $D = 1$ for individuals restricted to one of the primary tactics.

I assume that an individual's strategy is inherited from its parent (haploid population).

In the iteroparous (overlapping generations) version of the model, the probability of survival of an individual between consecutive time units is μ. Only survivors reproduce, and the number of offspring of individual i which survive to time unit $t+1$ is

$$\mathbf{Poisson}\left[\frac{(N - n_s(t))w(i,t)}{\sum w(j,t)}\right], \tag{3}$$

where $n_S(t)$ is the total number of survivors from time unit t to $t+1$, and the summation in the denominator is over these individuals. This gives density-dependence with equilibrium population size N ($=1{,}500$), and an expected reproductive rate of individual i at time t proportional to w(i,t).

In the semelparous (non-overlapping generations) version, each individual lives for one time unit, and may give birth to individuals in the next time unit, so a generation is one time unit. The number of offspring of individual i in the following generation $(t+1)$ is

$$\mathbf{Poisson}\left[\frac{N \cdot w(i,t)}{\sum w(j,t)}\right]. \tag{4}$$

Environmental trajectories were calculated with a variety of spectral types and levels of noise. Starting off with Gaussian white noise, in which each element is an independent normally distributed random variable with mean 0 and standard deviation 1, $Y(t = 1,\ldots,T)$, for any slope of the inverse of the noise frequency spectrum, ω, a new trajectory can be calculated:

$$y = \frac{\delta \cdot S^{-1}(S(Y)^{-\omega})}{\mathbf{SD}\left(S^{-1}(S(Y)^{-\omega})\right)}, \tag{5}$$

where S is the Fourier transform, and S^{-1} the inverse Fourier transform. The power frequency spectrum for white noise is flat, so that $S(Y)^{-\omega}$ produces an inverse power frequency spectrum with slope ω. δ gives y the desired variance.

Initially the population included 100 individuals of each of 15 learning types, each assumed to have a different parent, with intrinsic and target behavior $X = N(0,\sigma)$, and realized behavior $x = N(X,\sigma)$ for this parental generation. The model run proceeded until all remaining individuals were using the same learning strategy, or (more rarely; 22% of runs), if no learning strategy became universal, after T time units. For the iteroparous (overlapping generations) model, $T = 2^{14}$ ($=16{,}384$) time units, and for the semelparous (non-overlapping generations) model, in which evolution proceeded more rapidly, $T = 2^9$ ($=512$) time units. The semelparous model was also run with $T = 2^{14}$ for some parameter combinations, but results were similar, and are not presented.

One hundred sets of runs were made, each with a different T-element initial series of Gaussian white noise, Y, and each including one run with each combination of $\omega = -0.5, 0.0, 0.5, 1.0, 1.5, 2.0, 2.5$ (mild blue to very red noise), and $\delta = 0.125, 0.25, 0.5, 1, 2, 4, 8$ (scaled relative to q, the SD of the fitness function), so indicating situations ranging from when environmental variation has almost no effect on fitness to when its precise value is absolutely crucial. To incorporate parameter uncertainty, for each set of runs, values for survival and learning parameters were randomly chosen from the following possibilities:

Survival (just for iteroparous populations):
$\mu = \{0.75, 0.90, 0.95, 0.975, 0.99\}$;
Behavioral accuracy: $\sigma = \{0.08, 0.15, 0.25, 0.50, 0.75\}$;
Cost of vertical learning: $C_V = 1-\{0.01, 0.03, 0.05, 0.07, 0.1\}$;
Cost of horizontal/oblique learning:
$C_H = C_V-\{0.01, 0.03, 0.05, 0.07, 0.1\}$;
Cost of individual learning:
$C_I = C_H-\{0.01, 0.03, 0.05, 0.07, 0.1\}$;
Cost of contingency: $d = \{0.90, 0.93, 0.95, 0.97, 0.99\}$.

Results from runs in which each parameter was varied in turn, keeping the others constant, are presented in the Appendix.

For a given type of environment (defined by ω and δ) the success of a learning strategy was indicated by the mean proportion of the survivors with that strategy over the 100 runs in that environment. In most runs the survivors used just one strategy, but this successful strategy could vary between runs using the same set of parameters.

3. Results

For iteroparous (non-overlapping generations) populations in which individuals can reproduce during several time units, the evolution of learning occurs differently in three principal types of climate (Fig. 1(a)). With low amplitude environmental noise, having a standard deviation less than about 40% of the SD of the fitness

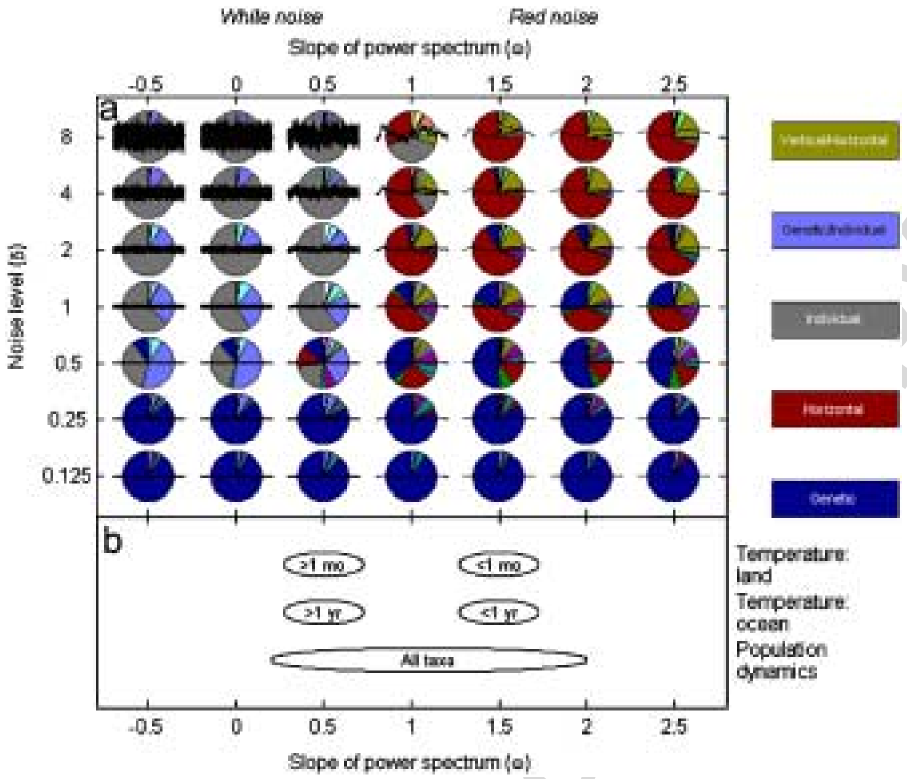

Fig. 1. Distribution of evolved learning strategies in different environmental conditions for the iteroparous (overlapping generations) model with randomly chosen learning and survival parameter values (a). Pie diagrams show mean proportions of persisting individuals with each learning strategy: 'Genetic' determination, 'Individual' learning, 'Vertical' and 'Horizontal' (horizontal/oblique) social learning, and contingent combinations. Strategies not shown in the legend accounted for less than 10% of the surviving individuals for any type of environmental noise. Representative trajectories for each type of environmental noise are overlaid. Approximate ranges of the inverse of the slope of the noise spectrum (ω) are shown in panel (b) for terrestrial thermal climates (Pelletier, 1997), oceanic thermal climates (Hall and Manabe, 1997; Timmermann et al., 1998; Leeuwenburgh and Stammer, 2001; Dommenget and Latif, 2002), and the population dynamics of organisms (Inchausti and Halley, 2002).

function, genetic determination is general. With high amplitude environmental "white" noise, with $\omega < \sim 0.7$, individual learning usually prevails. When the environmental noise is red ($\omega > \sim 0.7$) and of amplitude greater than the SD of the fitness function, then organisms usually employ social learning, generally oblique/horizontal but sometimes contingent strategies including vertical learning.

Variation in the input parameters modifies this picture in intuitively reasonable ways (see Appendix). Reducing the costs of individual learning, learning in general, or contingency increases the prevalence of the respective strategies, and vice versa. Additionally, with low costs of learning, pure individual learning becomes important at very high levels of red noise (at all values of ω). Substantial changes in behavioral accuracy, the ability of the learning tactics to produce behavior close to the environmental optimum, had relatively minor effects on the results.

For semelparous (overlapping generations) populations, in which individuals reproduce only once, the results are less consistent for high amplitude red noise (Fig. 2); individual learning or a contingent strategy including vertical social learning and individual learning often predominating. The latter is ironic in that vertical social learning will not be available to many semelparous organisms, whose parents are not likely be alive during the learning phase of the life cycle.

4. Discussion

4.1. The effects of failures in model assumptions

An important assumption of the model is that the accuracies of all basic learning tactics are taken to be equal. If they are not, the optimal strategy regions will be modified. For instance, if socially learned behavior is closer to the mean of the models' behavior than individually learned behavior is to the environmental optimum, then social learning will prevail in larger regions than suggested in Fig. 1(a) (Boyd and Richerson, 1985). Another simplification of the models is in using a haploid model of both the genetic determination of behavior and in the inheritance of learning strategy. However, as the primary advantage of genetic determination in this context is that it allows organisms to have similar behavior to the successful members of the previous generation at no cost, it seems unlikely that diploid inheritance would make any substantial difference to the results.

The model parameters are treated as fixed, but it is reasonable that the accuracy of a learning tactic (indicated

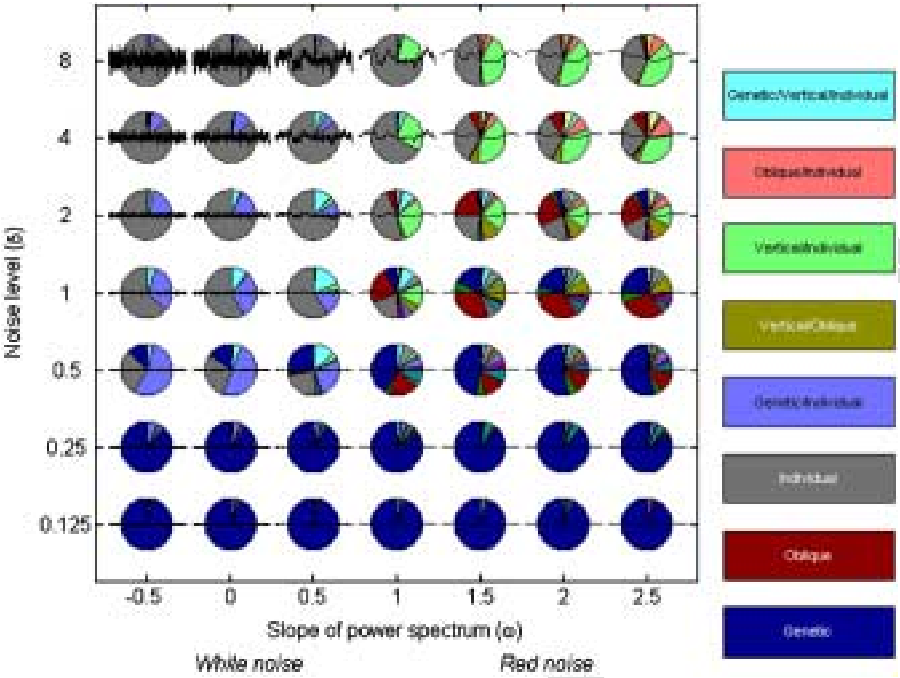

Fig. 2. Distribution of evolved learning after strategies in different environmental conditions for the semelparous (non-overlapping generations) model with randomly chosen learning and survival parameter values. Pie diagrams show mean persisting proportions of individuals with each learning strategy: 'Genetic' determination, 'Individual' learning, 'Vertical' and 'Oblique' social learning, and contingent combinations. Strategies not shown in the legend accounted for less than 10% of the surviving individuals for any type of environmental noise. Representative trajectories for each type of environmental noise are overlaid.

by 1/σ) and its cost (indicated by 1/C) may be positively related (Boyd and Richerson, 1985) on both ecological and evolutionary scales. However, as variation in neither σ nor C had much effect on the overall results (Appendix), I suspect that their linkage would also make little impact.

The models in this paper allow different learning strategies to compete on "an equal footing"—they initially have equal numbers of adherents. However, under some scenarios, horizontal/oblique learning faces an initial barrier: it is a good tactic when reasonably common, but a poor tactic when rare, as there are few useful models (Aoki and Feldman, 1987; Boyd and Richerson, 1996). This is particularly the case when social learning competes solely against a strategy of genetic determination. The way over this initial barrier is through individual learning. Individual learning, although costly, can outcompete genetic determination in variable environments (Figs. 1 and 2). Once common, it may provide a substrate of individuals with accurate behavior upon which less costly social learning strategies can evolve, although there may still be barriers (Boyd and Richerson, 1996), and other constraints to the evolution of social learning, such as cognitive substructure (Roper, 1986).

For many species, the fitness-determining environment may include several dimensions, such as temperature and rainfall. If all of the important environmental variables have similarly structured frequency spectra, then the most variable should determine the learning strategy. But, supposing, for instance, that for a marine organism temperature has high variance slightly red noise, and salinity lower variance but much redder noise (Hall and Manabe, 1997), then the situation becomes more complex, and I suspect that contingent strategies will be particularly favored.

In most forms of social learning, such as imitation and emulation, the costs primarily fall on the learner, and this is assumed in my simulations. However, teaching is a type of social learning in which the model incurs substantive costs (Caro and Hauser, 1992). If teaching is vertical (parent-offspring) or both teaching and being taught are circumscribed within one inherited learning strategy, then the models used here should be applicable. However, if those who do not possess the ability to teach benefit from being taught by non-relatives, then teaching will face barriers to its evolution in addition to those considered here.

4.2. Comparisons with previous results

Previous studies of the evolution of learning capacity (Boyd and Richerson, 1983, 1985, 1988, 1996; Feldman et al., 1996; Lachmann and Jablonka, 1996; Laland et al., 1996) were each only able to compare two or three (Aoki et al., 2005) strategies, used less realistic models of environmental variation, and their results are sometimes uncertain because of mathematical intractability (Aoki, 1991). Thus as a whole they cover only a small part of the scope of the current work. However, where available, the results of such analytical comparisons of pairs of strategies are generally in agreement with those from this more comprehensive analysis. These include a prevalence of genetic determination when environmental variability is very low (Cavalli-Sforza and Feldman, 1983; Boyd and Richerson, 1985; Aoki et al., 2005), and that individual learning may be more favorable than social learning when environments become very variable over short time-scales (Boyd and Richerson, 1988; Feldman et al., 1996; Laland et al., 1996).

Some earlier models (e.g. Feldman et al., 1996; Wakano et al., 2004; Aoki et al., 2005) predicted equilibrium mixed populations of individual and social learning, with the individual learners being needed to allow the social learners to track environmental change. However, a quite frequent outcome of my simulations (15% of runs for the iteroparous model, and 3% for the semelparous model) was a population consisting entirely of horizontal/oblique social learners (Figs. 1 and 2). Such a population cannot track environmental change in my models as the mean realized behavior of the population is stationary through time. This is illustrated in Fig. 3 by a quite typical run of the iteroparous model in a variable and red environment. Horizontal social learners initially increase in frequency, but then, for many generations, their frequency ranges between 95–99%, with a small proportion of individual learners, or those with contingent strategies, persisting and allowing the population's behavior to track the environment. However, once these few, but important, "tracking" individuals are gone, the behavior of the population stays nearly constant while the environment changes (Fig. 3). At this point, in reality, mean fitness declines dramatically and population extinction is likely (although this was not shown by my models which halted once one strategy had achieved domination). The removal of the last "tracking" individuals is a stochastic event, and will be less likely in populations larger than the 1,500 of my model, but these results both back up the importance of mixed populations found by earlier models, and also illustrate the dangers of complete cultural conformism in small populations, described so vividly for human societies by Diamond (2005).

Boyd and Richerson (1983, 1985) estimated that a strategy of social plus individual learning outcompetes one of genetic determination plus individual learning in variable environments when the environmental autocorrelation is greater than about 0.3, which with the 1/f models is achieved when $\omega \geqslant 0.23$. This is a little lower than when social learning becomes important in my results (Figs. 1 and 2), but 1/f noise possesses characteristics absent in autoregressive models, and the models in this paper allow organisms many more options.

4.3. The evolution of learning strategies

Although the costs of learning and contingency can affect the expected evolutionary outcome, the principal regions shown in Figs. 1(a) and 2 are quite robust, as they were derived using a range of parameter values but produced similar results (see also Appendix). Thus to

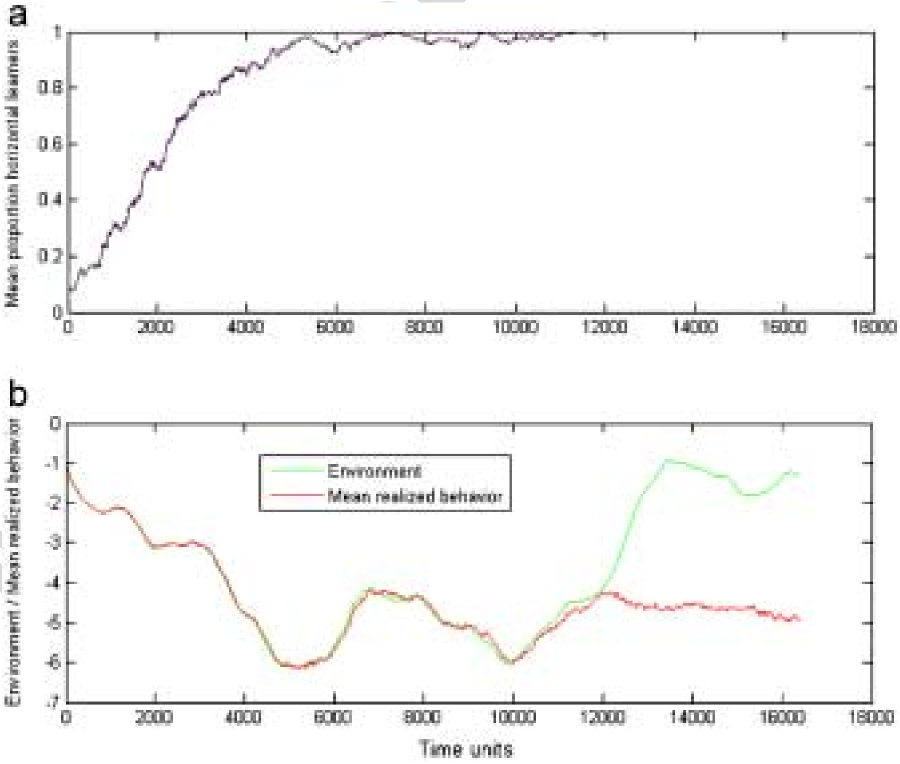

Fig. 3. The results of one run of the iteroparous model in a red and variable environment ($\omega = 2.0$ and $\delta = 4.0$) allowing the run to go 4,000 time units beyond fixation of the horizontal learning strategy (a) showing (b) the trajectories of mean environment (y) and mean realized population behavior. Once horizontal learning is fixed, population behavior no longer tracks environmental change.

estimate the most effective and likely-to-evolve learning strategy for a species principally requires knowledge of its environment. What are the environmental variables that most affect fitness and how do they vary both in magnitude, relative to the fitness function, and spectral characteristics?

While the level of environmental noise is relative to the width of the fitness function, and thus dependent on the autoecology of a species, the slope of the noise spectrum is a characteristic of a particular variable in a particular environment. I assume that the slope of the logged environmental noise spectrum is straight, giving pure 1/f noise. Environmental noise exponents usually change with frequency, although they are often fairly linear over large temporal scales (Hall and Manabe, 1997; Pelletier, 1997). The time periods over which an organism can store energy likely sets the lower limit of the range of time-scales important for evolutionary processes and the order of ten generations the upper limit (Richerson and Boyd, 2004).

Temperature is one of the most significant determinants of ecology (Begon et al., 1996). The power spectrum of temperature scales with $\omega = \sim 0.5$ at all except the smallest time-scales when $\omega = \sim 1.5$ (Fig. 1(b)). This reddening of the environment might suggest social learning being most adaptive in the shortest-lived, and generally smallest organisms. However, a consequence of the general redness in temperature variation is that environmental variation is low at very short time-scales, thus indicating genetic determination for short-lived organisms. Conversely the magnitude of lifetime environmental variation will be effectively larger for long-lived organisms, although this may be partially countered by wider fitness functions of the longer-lived species, which will generally be better able to buffer environmental variation through features such as endothermy, larger body size (Lindstedt and Boyce, 1985), or niche construction (Laland et al., 2000). If these buffering effects counter the increase in environmental variation with time scale, then genetic determination should also prevail, but more usually, I think, environmental variation will be large compared to the SD of the fitness function for long-lived organisms, and the model predicts that evolution should promote individual learning, or some other form of phenotypic plasticity that has characteristics indistinguishable from individual learning in my model (Agrawal, 2001). There appears to be little role for social learning in a thermally dominated environment.

However, temperature is not the only environmental dimension, and for many species the abundance of other species, especially predators, hosts and prey, will be the most significant determinants of fitness. Population series show a range of spectral exponents, but they are mostly red with a median exponent of $\omega = \sim 1.1$ (Inchausti and Halley, 2002; Fig. 1(b)). In Inchausti and Halley's study, larger species had generally redder population biology, and among taxonomic groups with reasonable sample sizes (>10), mammal populations were reddest (Inchausti and Halley, 2002). Thus, if patterns of population variability are indicative of environmental variability, the environments of larger, higher trophic level, animals, especially mammals, are likely redder than suggested by the spectral analysis of the thermal climate alone, and are in the range that favors social learning. Therefore social learning will likely have been most favored among large, long-lived and slowly reproducing mammals, and especially their predators. Also favored will be any other mechanism that transmits useful information in a parallel manner, such as maternal effects.

My results support Richerson and Boyd's (2004) hypothesis that increased climatic variation in the Pleistocene may have driven, at least partially, the evolution of sophisticated social learning in humans. Unfortunately, we do not know how levels and spectral characteristics of environmental variation at scales of months to decades have changed over most of the past million years, but inferences from lower frequency data indicate a general increase in conditions that would promote social learning (Richerson and Boyd, 2004).

Oceanic environments are structured somewhat differently from those on land. In the sea, very red ($\omega = \sim 1.5$) thermal environments are found at scales up to about a year (as compared to 1 month on land; Fig. 1(b)). Oceanic organisms with lifetimes of less than a few months live in very stable environments and so their behavior will tend to be genetically determined. Moving to longer-lived animals and up the food chain, environmental variability will increase, and trophic effects will likely increase redness for species higher on the food chain, as on land (Kaitala et al., 1997), but more so (Steele, 1985). Of the groups of species examined by Inchausti and Halley (2002), the secondary carnivore aquatic species had much the reddest population trajectories ($\omega \approx 1.5$; $n = 5$), and so the ocean might particularly favor social learning, especially among large marine mammals (Rendell and Whitehead, 2001).

Spatial variation in the environment can also be important (Boyd and Richerson, 1985, 1988). If, through active or passive movement, individuals are quite likely to live in environments very different from their parents, or to change environments during their lifetimes, then this will affect the efficacies of different behavioral control strategies. Horizontal social learning of local optimal conditions, or vertical social learning of optimal movement strategies, may be favored (Boyd and Richerson, 1988; Rendell and Whitehead, 2001). Oceanic environments have red temperature–distance spectra over scales up to about 5,000 km (Leeuwenburgh and Stammer, 2001), and the dynamics of marine fish populations are generally correlated over larger spatial scales than those in freshwater (Myers et al., 1997), both of which might indicate relatively greater benefits to social learning in the ocean.

5. Conclusion

The results of this study go beyond those from previous work in several respects. A two-dimensional space of environmental variability, that likely includes good approximations for most real environments, is mapped for the types of behavioral determination most likely to evolve. A wide range of strategies is considered. In some areas of this map, there are clear and consistent results over a wide range of parameter values, especially that genetic determination should predominate with low environmental variation, that individual learning is likely to evolve in environments with much high-frequency noise, and social learning where variation is dominated by low frequencies. While these main results are both intuitive and indicated by previous analytical models, this analysis is much more explicit about the boundaries of the principal regions of the map. Because one of the axes of the environmental variation space, ω, is measurable, and values are available for real environments, the results of the modelling can be translated into fairly precise predictions for the type of behavioral determination of a species as a function of the principal environmental determinants of fitness. So, for instance, I am able to conclude that learning is more likely to evolve in long-lived animals, and that, among long-lived animals, we should expect generally more social learning at higher trophic levels, and in marine species.

However, this is just a start, and there is much more useful work that could be done with this kind of model. Some possibilities have been indicated earlier in the discussion. For instance, it is simplistic and unrealistic to have all learning strategies starting off on an equal footing. The ability of more complex strategies to invade populations dominated by simpler, ancestral, strategies needs investigation, as do the conditions for the collapse of populations when social learning becomes universal (Fig. 3). Another instance where additional modeling would be desirable is in the evolution of cost-accuracy profiles within learning tactics.

For particular species, this approach could also be developed by investigating which principal sources of environmental variation affect fitness. These sources could then be analysed using the 1/f approach, and the predictions of the model compared with actual studies of behavioral determination. This would be even more informative if carried out across several related species.

Acknowledgments

This research was supported by the Natural Sciences and Engineering Research Council of Canada. Many thanks to Andrew Horn, Katie McAuliffe, Ransom Myers, Luke Rendell, Peter Richerson and the reviewers for very helpful suggestions.

Appendix. Effects of parameter variation

To investigate the effects of parameter variation on the results of the model, 20 sets of runs, each containing all

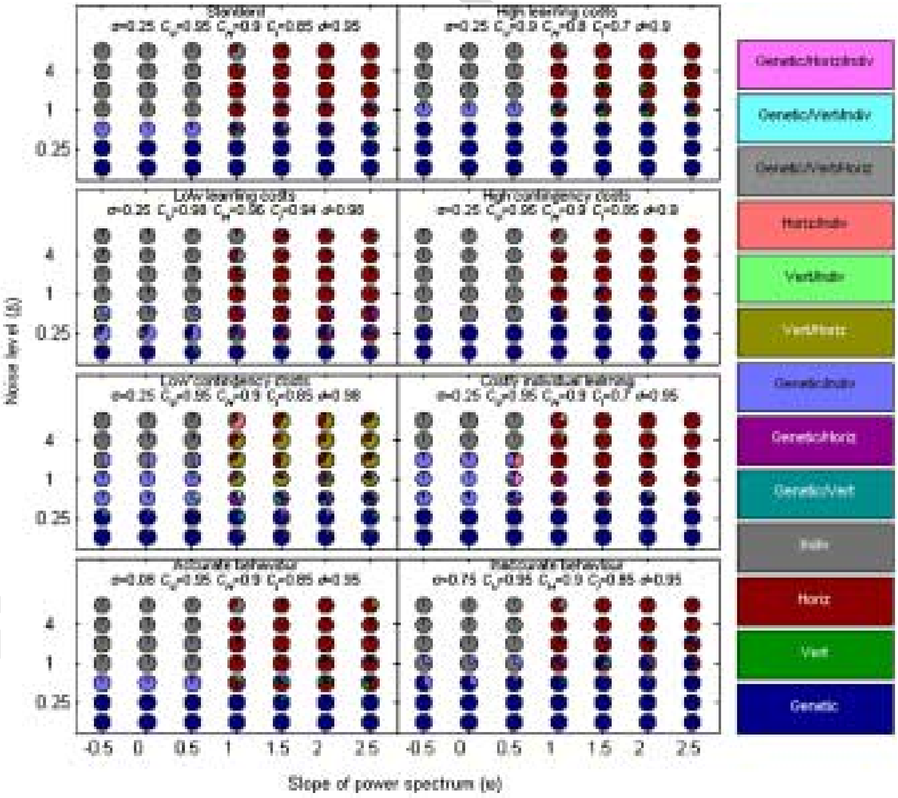

Fig. 4. Effects of parameter variation on results of iteroparous (overlapping generations) model. Each panel represents the results of running the model with a different set of parameters. The pie diagrams show the mean proportion of individuals with each learning strategy over twenty random runs. ('Genetic' = genetic determination; 'Indiv' = individual, 'Vert' = vertical, and 'Horiz' = horizontal/oblique social learning.) All strategies not shown in the legend on the right accounted for less than 10% of the surviving individuals for any type of environmental noise and set of parameters.

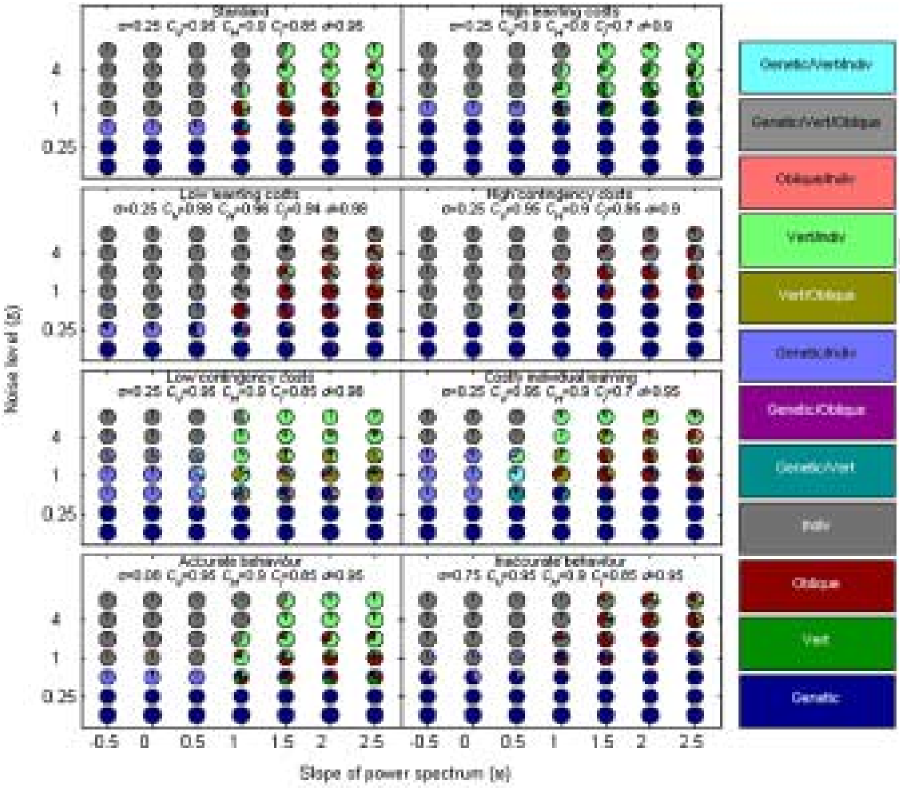

Fig. 5. Effects of parameter variation on results of semelparous (non-overlapping generations) model. Each panel represents the results of running the model with a different set of parameters. The pie diagrams show the mean proportion of individuals with each learning strategy over 20 random runs. ('Genetic' = genetic determination; 'Indiv' = individual, 'Vert' = vertical, and 'Oblique' = oblique social learning.) All strategies not shown in the legend on the right accounted for less than 10% of the surviving individuals for any type of environmental noise and set of parameters.

combinations of $\omega = -0.5, 0.0, 0.5, 1.0, 1.5, 2.0, 2.5$, and $\delta = 0.125, 0.25, 0.5, 1, 2, 4, 8$, were made with a "standard" set of parameters ($\mu = 0.975$; $\sigma = 0.25$; $C_V = 0.95$; $C_H = 0.90$; $C_I = 0.85$; $d = 0.95$), as well the following variants:

"High learning costs": $\sigma = 0.25$; $C_V = 0.90$; $C_H = 0.80$; $C_I = 0.70$; $d = 0.90$.
"Low learning costs": $\sigma = 0.25$; $C_V = 0.98$; $C_H = 0.96$; $C_I = 0.94$; $d = 0.98$.
"High contingency costs": $\sigma = 0.25$; $C_V = 0.95$; $C_H = 0.90$; $C_I = 0.85$; $d = 0.90$.
"Low contingency costs": $\sigma = 0.25$; $C_V = 0.95$; $C_H = 0.90$; $C_I = 0.85$; $d = 0.98$.
"Costly individual learning": $\sigma = 0.25$; $C_V = 0.95$; $C_H = 0.90$; $C_I = 0.70$; $d = 0.95$.
"Accurate behavior": $\sigma = 0.08$; $C_V = 0.95$; $C_H = 0.90$; $C_I = 0.85$; $d = 0.95$.
"Inaccurate behavior": $\sigma = 0.75$; $C_V = 0.95$; $C_H = 0.90$; $C_I = 0.85$; $d = 0.95$.

Results for the different parameter combinations are shown in Figs. 4 and 5 for the iteroparous (overlapping generations) and semelparous (non-overlapping generations) models, respectively.

References

Agrawal, A.A., 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294, 321–326.

Aoki, K., 1991. Some theoretical aspects of the origin of cultural transmission. In: Osaua, S., Honjo, T. (Eds.), Evolution of Life: Fossils, Molecules and Culture. Springer, Tokyo, pp. 439–449.

Aoki, K., Feldman, M.W., 1987. Toward a theory for the evolution of cultural communication: coevolution of signal transmission and reception. Proc. Natl. Acad. Sci. USA 84, 7164–7168.

Aoki, K., Wakano, J.Y., Feldman, M.W., 2005. The emergence of social learning in a temporally changing environment: a theoretical model. Curr. Anthrop. 46, 334–340.

Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology. Individuals, Populations and Communities, third ed. Blackwell Science, Oxford, UK.

Boyd, R., Richerson, P.J., 1983. The cultural transmission of acquired variation: effects on fitness. J. Theor. Biol. 100, 567–596.

Boyd, R., Richerson, P., 1985. Culture and the Evolutionary Process. Chicago University Press, Chicago.

Boyd, R., Richerson, P., 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. In: Zentall, T., Galef, Jr., B.G. (Eds.), Social Learning: Psychological and Biological Perspectives. Lawrence Erlbaum Association, Hillsdale, NJ, pp. 29–48.

Boyd, R., Richerson, P.J., 1996. Why culture is common, but cultural evolution is rare. Proc. Br. Acad. 88, 77–93.

Caro, T.M., Hauser, M.D., 1992. Is there teaching in non-human animals? Quart. Rev. Biol. 67, 151–174.

Cavalli-Sforza, L.L., Feldman, M.W., 1983. Cultural versus genetic adaptation. Proc. Natl. Acad. Sci. USA. 80, 4993–4996.

Diamond, J., 2005. Collapse: How Societies Choose to Fail or Succeed. Penguin, New York.

Dommenget, D., Latif, M., 2002. Analysis of observed and simulated SST spectra in the midlatitudes. Clim. Dyn. 19, 277–288.

Feldman, M.W., Aoki, K., Kumm, J., 1996. Individual versus social learning: evolutionary analysis in a fluctuating environment. Anth. Sci. 104, 209–231.

Gisiger, T., 2001. Scale invariance in biology: coincidence or footprint of a universal mechanism? Biol. Rev. 76, 161–209.

Hall, A., Manabe, S., 1997. Can local linear stochastic theory explain sea surface temperature and salinity variability? Clim. Dyn. 13, 167–180.

Halley, J.M., 1996. Ecology, evolution and 1/f noise. Trends Ecol. Evol. 11, 33–37.

Inchausti, P., Halley, J., 2002. The long-term temporal variability and spectral colour of animal populations. Evol. Ecol. Res. 4, 1033–1048.

Kaitala, V., Ylikarjula, J., Ranta, E., Lundberg, P., 1997. Population dynamics and the colour of environmental noise. Proc. Roy. Soc. London B. 264, 943–948.

Lachmann, M., Jablonka, E., 1996. The inheritance of phenotypes: an adaptation to fluctuating environments. J. Theor. Biol. 181, 1–9.

Laland, K.N., Richerson, P.J., Boyd, R., 1996. Developing a theory of animal social learning. In: Heyes, C.M., Galef, B.G.J. (Eds.), Social Learning in Animals: The Roots of Culture. Academic Press, San Diego, California, pp. 129–154.

Laland, K.N., Odling-Smee, J., Feldman, M.W., 2000. Niche construction, biological evolution and cultural change. Behav. Brain Sci. 23, 131–175.

Leeuwenburgh, O., Stammer, D., 2001. The effect of ocean currents on sea surface temperature anomalies. J. Phys. Oceanogr. 31, 2340–2358.

Lefebvre, L., Palmeta, B., 1988. Mechanisms, ecology, and population diffusion of socially- learned food-finding behavior in feral pigeons. In: Zentall, T.R., Galef, B.G. (Eds.), Social Learning: Psychological and Biological Perspectives. Lawrence Erlbaum, Hillsdale, NJ, pp. 141–165.

Lindstedt, S.L., Boyce, M.S., 1985. Seasonality, fasting endurance, and body size in mammals. Am. Nat. 125, 873–878.

Myers, R.A., Mertz, G., Bridson, J., 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Can. J. Fish. Aquat. Sci. 54, 1400–1407.

Pelletier, J., 1997. Analysis and modeling of the natural variability of climate. J. Clim. 10, 1331–1342.

Rendell, L., Whitehead, H., 2001. Culture in whales and dolphins. Behav. Brain Sci. 24, 309–324.

Richerson, P.J., Boyd, R., 1998. The evolution of human ultrasociality. In: Eibl-Eibesfeldt, I., Salter, F.K. (Eds.), Indoctrinability, Ideology and Warfare. Berghahn Books, London, pp. 71–95.

Richerson, P.J., Boyd, R., 2004. Not by Genes Alone: How Culture Transformed Human Evolution. University of Chicago Press, Chicago, IL.

Roper, T.J., 1986. Cultural evolution of feeding behaviour in animals. Sci. Prog. 70, 571–583.

Steele, J.H., 1985. A comparison of terrestrial and marine ecological systems. Nature, Lond 313, 355–358.

Timmermann, A., Latif, M., Voss, R., Grötzner, A., 1998. Northern hemispheric interdecadal variability: a coupled air-sea mode. J. Clim. 11, 1906–1931.

Wakano, J.Y., Aoki, K., Feldman, M.W., 2004. Evolution of social learning: a mathematical analysis. Theor. Popul. Biol. 66, 249–258.