The Baldwin veering effect: How intelligence can change the course of evolution.

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Abstract

The effect of phenotypic plasticity in an evolutionary process, the so-called Baldwin effect, has been studied extensively for more than 100 years. Plasticity has been found to influence the speed of evolution towards an optimal genetic configuration, but whether or not plasticity can cause evolution to veer towards a different genetic configuration from what pursued by evolution alone, is still an open question. Here, this question is investigated analytically and experimentally, by means of an agent-based simulation of a foraging task, in an environment where the distribution of resources follows seasonal cycles. Foraging is limited by a trade-off that forces agents to either specialize to one specific resource type or generalize over all resource types at a lower success rate. Experiments demonstrate that in such an environment the introduction of learning, one of many instances of phenotypic plasticity, leads evolution to a different genetic configuration. Specifically, learning individuals develop a generalist strategy, which allows to adapt quickly to changes in the resource distribution, under the same conditions for which non-learners would develop a specialist strategy, which maximizes the foraging efficiency for a specific resource type. This paper expands the literature at the interface between Biology and Machine Learning by identifying the Baldwin effects in cyclically-changing environments and demonstrating that learning can change the outcome of evolution. The models introduced in this work might prove useful in other cyclically-changing contexts beyond the field of Biology e.g. opinion formation and polarization.

1 Introduction

The so called Baldwin effect [1] is a much debated finding in the literature of evolution [2]. The Baldwin effect is used to explain how new features,
acquired by an individual by means of phenotypic plasticity [3, 4, 5], are encoded into the genome by natural selection. Baldwin proposed this new mechanism of evolution to explain how complex features such as an eye can evolve [6, 7, 8], as an alternative to the then-popular Lamarckian evolution, which assumed that traits acquired by an individual through phenotypic plasticity would be transferred directly to its offspring’s genome [9]. Learning, i.e. an instance of phenotypic plasticity [10, 11, 12], has been found to affect how evolution reaches an optimal configuration [13, 14] by either speeding up [15] or slowing down the evolutionary process [2, 16].

This work brings that concept a step further by demonstrating that learning can change the outcome of the evolutionary process. We study the effect of learning on evolution both experimentally, by means of an Agent-Based simulation of a foraging task [17, 18], and analytically, by means of a formal mathematical model [19]. Our choice of model favored simplicity over realism, modeling realistic entities and ecosystems is outside the scope of this work.

The environment cycles periodically between two different configurations, named “seasons” [20, 21, 17], which determine what resources are available for agents to forage. An agent’s “skill” value determines the trade-off between the foraging success of the two resource types [22]: the more an agent specializes in one resource, the less effectively it can forage the other resource, e.g. due to neophobia [23], a non-transferable skill set or other constraints, e.g. energy or memory constraints. Learning allows the skill level, which determines the evolutionary fitness, to change from the genetically-defined innate value to a value more suited to the current configuration of the environment.

Our computational experiments demonstrate the existence in a cyclical environment of the Baldwin expediting effect [13, 24], i.e. faster evolutionary convergence, and of the Baldwin delaying effect [2], i.e. slower evolutionary convergence. Further experimental and analytical results demonstrate that learning is not only able to condition the speed of convergence but also the evolved genetic configuration; this new effect is named “Baldwin veering effect”. Specifically it is found that learning leads to the evolution of a generalist foraging behavior under the same conditions where evolution alone would converge to a specialist foraging behavior. Analytical results confirm that learning changes the fitness landscape in a way that makes a generalist strategy a global optimum towards which evolution converges. The intuition is that non-learning agents cannot adapt to the fast changes in the environment, so they maximize their foraging efficiency for one type of resource. Conversely, learning agents can adapt to any environmental condition, and a generalist strategy offers them higher flexibility.
The main contributions of this paper are to show that in a cyclically changing environment: (I) the well-known Baldwin expediting and delaying effects are present, (II) learning affects the outcome of the evolutionary process by driving evolution to a different configuration, we name this the “Baldwin veering effect”, (III) a formal mathematical model that we introduce captures this new effect and confirms our experimental findings, and (IV) the existence of this new effect is conditioned only upon the relation between the speed of learning and the frequency of change in the environment.

These results are relevant for the literature of Biology, as they expand the understanding of how phenotypic plasticity influences evolution and open up a novel dimension for the study of the interaction between learning and evolution. The results are also interesting from a sociological perspective as they might help to understand how technology, e.g. machine learning, might be used to influence opinion formation and polarization by mediating the rate of exposure to different opinions [25, 26, 27].

This paper is structured as follows: Section 2 presents details of the agent based methodology, the environmental setting and the learning mechanisms used for the computational experiments, Section 3 presents the design and results of the experiments substantiating the claims in this paper, Section 4 introduces the analytical model and describes results that validate our experimental findings, Section 5 presents a short discussion and Section 6 provides concluding remarks to this work.

2 Computational model

In this paper we develop an agent-based simulation framework [28] in which a population of software agents performs a foraging task [29, 17, 30] and is subjected to an evolutionary process. In the evolutionary simulation, natural selection is driven by each agent’s evolutionary fitness which is assumed to be directly proportional to its energy level. The energy level of an individual depends on three factors: (i) the configuration of the environment which determines the availability of resources at each given time, (ii) the skill level which determines the probability of successful foraging, and (iii) the behavior which determines what actions to execute for a given configuration of the environment. The birth and death of agent is governed by a roulette wheel algorithm with stochastic acceptance (as in [31]).

We study two types of agents: reactive agents keep their inherited behavior and skill level constant throughout their lifetime, while learning agents
adapt according to their experience via reinforcement learning [40, 41, 18, 42]. Different reinforcement learning architectures are evaluated: QLearning [43], reinforcement learning based on a Restricted Boltzman Machine [44], Deep Reinforcement Learning [45], and reinforcement learning based on a single feed forward perceptron (see also Appendix III.2). A population of reactive agents is shaped by evolution, while a population of learning agents is shaped by the interaction between evolution and learning.

The environment is rendered dynamic by introducing two resource types and by varying their proportion over time [20] such that in every season a specific resource is more abundant than the others. Proficiency in both skills would allow agents to forage effectively in every season, our experimental design specifically prevents this by assuming a trade-off between the skill levels: agents can either become generalists, i.e. be able to forage both resources with a low probability, or specialize, i.e. be able to forage one resource with a high probability and loose the ability to forage the other.

The degree of specialization of a population is measured with different metrics: (I) the distribution of individual skill levels across the population, according to which a higher frequency of extreme skill levels corresponds to a more specialized population, (II) the individual foraging history, i.e. the frequency of successful foraging actions for a specific resource type, according to which extreme values indicate a specialized diet, (III) standard measures of group behavior that quantify the rate of consumption of resources. These measures and the details of the model are explained more formally in Appendix I.

3 Results of the computational experiments

3.1 The Baldwin expediting and delaying effects

Previous work in the literature defined two different effects: the Baldwin expediting effect, according to which learning makes genetic adaptation faster at reaching the optimum, and the Baldwin delaying effect, according to which learning reduces the speed of genetic adaptation. Previous studies conclude that the same model can show both effects, depending on the parameters of the learning mechanism, the fitness function and the starting conditions of the population [2].

The goal of this experiment is to verify whether or not either effect exists in a cyclical environment, a question that, to the best of our knowledge, has not been answered before [19].

The existence of the Baldwin effect is evaluated by comparing the speed
of adaptation of individual's genetic configurations to changes in the environment. Three populations of agents are compared:

- A population of reactive agents, i.e. unable to learn, is taken as baseline.
- A population of agents which can modify their own actions through learning (expediting).
- A population of agents which can modify their own actions and their skill level through learning (delaying).

Fig. 1 shows that the Baldwin effect is present as the speed of the genetic adaptation is affected by learning. Both the Baldwin expediting and delaying effect are visible. Learning allows agents to adapt their actions during their lifetime. By learning the correct mapping between actions and perceptions, agents improve their foraging capacity over time. Depending on the inherited skill level, learning can take more or less time. This difference allows the selection mechanism to differentiate between skill levels, thus producing the expediting effect. If learning is also able to adapt the skill level, its initial value becomes less crucial for the individual’s fitness: after a certain amount of learning iterations, all agents will have the same skill value, hence similar fitness. This has the effect of flattening the fitness landscape which makes natural selection less efficient at selecting the best initial skill levels, thus producing the delaying effect.
Figure 1: **The Baldwin effects.** Evolution of skill level over time in two different learning populations, compared to a population of reactive agents. The speed of adaptation changes with respect to the baseline, depending on the configuration of the learning algorithm, demonstrating both the Baldwin expediting and the Baldwin delaying effects. The vertical line indicates a change of season. Confidence intervals at the 95% confidence level are not shown as their size is negligible.

### 3.2 A new effect: the Baldwin veering effect

This experiment investigates whether the Baldwin veering effect exists, i.e. learning leads evolution towards a different outcome. The novelty of our work is to show that plasticity alone can affect the outcome of evolution, without requiring social interactions between populations [32, 33].

The intuition is that evolution and learning traverse the same space of genetic configurations, but with two different timescales. Evolution is able to adapt to slowly-changing environments, and learning might speed up or delay this process. If instead the environment changes too quickly for evolution to adapt, learning and evolution do not merely tend to the same objective but instead take on two different roles: Learning optimizes the behavior of individuals in response to environmental variability, while evolution optimizes
the learning process. The learning process can be optimized by evolving a starting point that minimizes the initial learning effort. Given that an individual can be born in either season, this optimal value is expected to be equidistant from the seasonal optima.

This prediction is verified by comparing the genetic configuration of the skill level across two different populations, one of learning agents and one of reactive agents. The Baldwin veering effect is present if the two populations develop a different genetic configuration, namely the reactive population specializes in either resource types while the learning population develops a generalist configuration.

Fig 2 shows that a population of reactive agents converges to extreme skill values, thus each half of the population specializes in foraging one type of resource. A learning population instead converges to an intermediate skill value, which allows to adapt quickly to any environmental condition. Fig 3 highlights the difference between genetic configurations developed by the two populations.
Figure 2: Comparison of the time history of the skill distributions across experiments. The skill level evolves to two different configurations, confirming that learning can change the outcome of evolution.
Figure 3: Comparison of end skill distribution across experiments. Lines indicate how often a given skill level occurs in the population. Experiments result in two different distributions, confirming that learning can change the configuration to which evolution converges. Each line represents the average genetic configuration over the last 1000 time steps of a simulation. Shaded areas represent confidence intervals at the 95% confidence level.

In order to verify that a difference in genetic configuration actually results in different behaviors, the agents that are alive during the last timestep of the simulation are cloned and used to initialize a new set of simulations. In these new simulations, the environment is set to have only one season and contains an equivalent quantity of both types of resources. Furthermore, agents do not reproduce and their behavior is fixed and fully determined by their genome. These new experiments are used to compute the measures of foraging history and of group behavior.

The measure of foraging history shows that the behaviors in the two conditions differ (cf. Fig 4), namely the reactive population splits in two groups of comparable size, each of which specializes in foraging one type of
resource, while the learning population has a more uniform foraging pattern which includes more generalists. The measure of foraging history of each agent is quantified by the frequency of foraging resources of type one, e.g. a value of 90% indicates that 90% of all resources foraged by the agent were of type one, and the remaining 10% of type two. These values are then aggregated across the population to determine the frequency of different values of foraging history.

Figure 4: **Foraging history comparison.** The lines represent the percentage of agents in the population which have a given foraging history value. Distributions of foraging actions resemble the distributions of skills, confirming that different genetic configurations lead to different actual behaviors. Dashed lines represent baseline populations, where all agents have skill level of 0.5 (Generalist) or half of the population has skill level 0.05 and the other half 0.95 (Specialist). Shaded areas (of negligible size) represent confidence intervals at the 95% confidence level.

Besides the measure of foraging history, different standard measures of group behavior [34, Pag. 241] are used to compare the behavior of the popu-
lations (cf Fig 5 and Appendix II for a description of the measures). The interpretation of these measures is not straightforward, so baselines are added for reference: the dashed line represents the value of a population where half of the agents specialize in one resource and the other half in the other resource, while the continuous line represents a population of generalists.

The measures confirm the results: the learning population displays a generalist behavior, both at the group level (Among-Resource Diversity) and at the individual level (Within-Individual Diversity), while individuals of the reactive population evolve a more specialized behavior. The result is not so clear for the group level of a reactive population, but it can be explained by including the result at the individual level: The measure of Among Resource Diversity (ARD) is high either if different individuals have different specialized diets or if individuals generalize, and the result of Within Individual Diversity (WID) exclude the latter cause.
Figure 5: Measures quantifying the behavior of the population. Left: Among Resource Diversity quantifies the behavior of the population, both populations display a similar generalist behavior. Right: Within Individual Diversity quantifies the behavior of individual agents, learning agents behave more generalist than reactive agents. The solid line represents a baseline population in which all agents have skill level 0.5, the dashed line represents a baseline population in which each half of the agents has skill level of 0.05 and 0.95 respectively.

4 Analysis of the mathematical model

The results outlined in the previous section showcase the existence of the Baldwin veering effect, but give little information about the process behind it. This section introduces and analyzes the predictions of an analytical model, inspired on previous work [35], which give a possible explanation to the simulation results and identify the conditions under which the Baldwin veering effect manifests. The model captures the individual fitness of agents through the definition of a general fitness function, the evolutionary process is not explicitly modeled so evolutionary outcomes are inferred from considerations about the relative fitness of different individuals. More fine-grained
results about evolution and its dynamics might be obtained by pairing the
fitness function with any existing model of evolution, e.g. [36, 35], such effort
is outside the scope of this paper and is left for future work.

The environment contains two types of resources, whose proportion is
denoted by $a_0$ and $a_1$.

The fitness of an individual $i$ is formulated as follows:

$$W_i = a_0 \cdot r_{i,0} + a_1 \cdot r_{i,1} = a_0 \cdot s_{i,0}^q + a_1 \cdot s_{i,1}^q$$

Where the foraging success $r_{i,j} = s_{i,j}^q$ is determined by the individual’s
skill level $s_{i,j} \in [0, 1]$ and by a parameter $q \in \mathbb{N}_{\geq 0}$ which defines the relation
between skill and foraging success. If the parameter $q = 1$, specializing on
one resource and generalizing on two resources lead to the same foraging
success. If $q > 1$ specialization is more beneficial as intermediate skill levels
produce a lower foraging success than extreme ones, vice versa if $q < 1$
generalization becomes more beneficial than specialization.

Following the design of the computational model, we assume that the two
skill levels of an individual are complementary, $s_{i,0} + s_{i,1} = 1$ as well as the
resource availability $a_1 + a_0 = 1$. Therefore, the notation can be simplified
by defining $s_i := s_{i,0}$ and $1 - s_i := s_{i,1}$.

$$W_i = a_0 \cdot s_i^q + (1 - a_0) \cdot (1 - s_i)^q$$ \hspace{1cm} (1)

In order to model the effect of learning agents, a new parameter $\delta$
is introduced which represent plasticity. A learning agent is not constrained
by its genetically defined skill level, which can be adapted to the conditions
of the environment. The value of $\delta$ determines the range of skill levels an
individual can express, this range is centered in the skill level and spans in
both direction (cf. Fig 6).

$$W_i = a_0 \cdot \min(1, (s_i + \delta))^q + (1 - a_0) \cdot \min(1, (1 - s_i + \delta))^q - c \cdot \delta$$ \hspace{1cm} (2)

The parameter $c$ determines the cost of plasticity [37]. The adapted skill
level cannot extend beyond the domain $[0, 1]$, hence the bounding to 1.
Figure 6: **Examples of plasticity ranges** for different skill levels and a fixed value of δ.

It is assumed that an agent can choose the best skill level available for each resource type right from the start with no delay, i.e. skill value of $s_i + \delta$ for resource type $a_0$ and skill value of $s_{i,1} + \delta = 1 - (s_i - \delta)$ for resource type $a_1$, which maximize the fitness function. Learning requires time to adapt, but our model is static, so this delay is modeled by reducing the value of δ (cf. Fig 7). In practice the value of δ depends on the ratio between the speed of learning and the season length: a slower learning mechanism reduces the distance to which the value can change, similarly a shorter season reduces the number of experiences an individual can have during a season.
Figure 7: **Modeling assumptions sketch.** The shaded area represents the cost of adaptation: the loss of fitness caused by adapting to the environment with respect to an already adapted individual. Learning requires time to adapt, defined by the speed of learning $\alpha$. This delay is modeled by reducing the plasticity $\delta$ such that the size of area $A$ is the same.

Figure 8: **Fitness for different combinations of skill level and $\delta$ for $q > 1$ and $c > 0$**. A value of $q$ larger than one implies that extreme skill levels deliver higher fitness than intermediate levels. The red circles represent the optimal skill values that maximize fitness for a given value of $\delta$. The optimal skill values start at the extremes for $\delta = 0$ and converge towards the center as $\delta$ increases, while for $\delta > 0.5$ fitness is maximized by a range of skill values which includes intermediate and extreme values. Note that the overall fitness of learning agents becomes higher than that of specialists with increasing values of $\delta$ and that fitness is maximized for $\delta = 0.5$. Also note that the introduction of learning, i.e. $\delta > 0$, changes the skill value for which fitness is maximized, i.e. the configuration towards which evolution converges. Left: $a_0 = 0.5$, right: $a_0 = 0.6$. 

(a) Results for $a_0 = 0.5$.  
(b) Results for $a_0 = 0.6$. 

0.0 0.2 0.4 0.6 0.8 1.0
Skill level
0.0 0.2 0.4 0.6 0.8 1.0
Skill level
0.0 0.2 0.4 0.6 0.8 1.0
Skill level
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Skill level
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Skill level
Fig 8 shows how different skill levels compare, in terms of fitness, for varying values of $\delta$. The red circles represent the globally optimum skill levels for a given value of $\delta$. If $\delta < 0.5$ the evolutionary process results in a population of specialists, while a population of generalists evolves if $\delta = 0.5$.

Note that the configuration with $\delta = 0.5$ and a skill level $s_i = 0.5$ maximizes the fitness as it allows agents choose any skill value in the range $[0, 1]$, hence forage both resource types with certainty. This confirms the existence of the “Baldwin veering effect” as any value of $\delta > 0$ produces a change in the fitness landscape hence a change in the skill value that maximizes fitness and is therefore selected by evolution. For values of $\delta > 0.5$ the agents might specialize again, as an increasingly large range of skill values produce the same fitness, but we can expect that not to happen if the plasticity cost is greater than zero \[37\]. These results are confirmed also for $c = 0$ and $q \leq 1$, see Appendix I.1

Concluding, learning agents evolve an intermediate skill level, i.e. a generalist configuration, only if learning speed is proportionate to the season length such that agents can adapt to both resource types. This result is general and hold independently of the level of $q$ and resource proportion $a_0$, hence confirms that the Baldwin veering effect depends exclusively on the timescales of learning and environmental change.

Future work will focus on verifying the predictions of the analytical model within the agent based simulation framework, in particular we expect to find a configuration in which the learning population splits in two groups of specialists with skill values in $[0, 0.5]$ and $[0.5, 1]$ respectively, and a configuration in which learning population develops a uniform distribution of skill values.

5 Discussion

Learning and evolution operate at two different timescales: The genetic configuration is changed by random mutations during the transmission of genes from parent to offspring, and mutations providing better fitness spread by natural selection over many successive generations. Learning agents are able to adapt their behavior and skill level after each successful foraging action, i.e. on a much shorter time scale, thus the behavior can radically change during the lifetime of an individual.

Two models with different levels of complexity and expressiveness are used. The existence of the Baldwin expediting and delaying effects are successfully reproduced in the computational model of a cyclic environment and the new Baldwin veering effect is found in both. Furthermore, formal anal-
ysis confirms these findings and identifies what preconditions are needed for the presence of this effect.

Our work is constrained to simple models with only two resources, we favored simplicity over realism, as the aim was to provide a proof of concept. Increasing the complexity of the environment, as well as introducing group behavior, is required to model any realistic ecosystem and is left for future work.

6 Conclusions

Learning is known to influence the speed at which evolution converges to some optimal configuration. This work, in contrast, addresses the question of whether learning can influence the genetic configuration selected by evolution. Following previous work, this question is answered by means of an agent-based simulation of a foraging task, with cyclical variability in the resource distribution. Additionally this result is confirmed through an analytical model.

Our work shows the existence of the Baldwin effect in a cyclical environment and identifies the novel “Baldwin veering effect” and the conditions under which it exists. More specifically we find that learning agents, whose speed of learning is proportionate to the cyclical change of the environment, evolve a generalist foraging strategy in the same conditions where reactive agents would develop a specialized foraging strategy. A formal model verifies that learning changes the fitness landscape such that a generalist strategy becomes the global optimum.

If the frequency of change in the environment is higher than the timescale at which evolution operates, evolution alone is unable to adapt to the changes, so agents specialize to forage one specific resource. Learning operates at a faster timescale than evolution, thus learning agents are able to adapt to a quickly changing environment and evolve a generalist configuration, as the role of evolution changes from optimizing the behavior to optimizing the flexibility of the learning algorithm.

Besides the implication for research in Biology and Evolution, our results might prove useful in other context which have a cyclical component, for example opinion formation and polarization: Opinion polarization is affected by the degree of exposition to contrasting information \cite{25, 38, 26}, e.g. echo chambers, which is in turn mediated by technology, e.g. machine learning \cite{27, 39}, which operates at a much faster timescale than human reasoning.
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Appendix

I  Formal definition of the model.

| Math symbol | Description |
|--------------|-------------|
| $\mathcal{A} = \{a_0, ..., a_N\}$ | The set of all $N$ agents ever alive in the simulation |
| $T = \{t \in \mathbb{N}_{0 \leq L}\}$ | The time steps, $t$ of the simulation |
| $\mathcal{A}^t = \{a \in \mathcal{A} : a \text{ is alive at timestep } t\}$ | The population at time $t$ |
| $s_t^a \in [0,1] : a \in \mathcal{A}^t$ | The skill level of agent $a$ at time $t$ |
| $R = \{r_0, ..., r_M\}$ | The set of $M$ resource types |
| $f(a, t) : \mathcal{A}^t \times T \to \mathbb{R}$ | The fitness function |
| $g(a, s_t^a, r) : \mathcal{A}^t \times \mathbb{R}_{\geq 0, \leq 1} \times R \to \{0, 1\}$ | The foraging success function of agent $a$ for resource type $r$ |
| $\epsilon \in \mathbb{R}$ | Energy level increased by successful foraging |
| $E_t^i = \{\phi_{i,r}^t : 1 \leq i \leq m \times m, r \in R\}$ | The configuration of the environment at time $t$ |
| $\phi_{i,r}^t \in \mathbb{N}_{\geq 0}$ | The quantity of resources of type $r$ in cell $i$ at time $t$ |
| $B(a,t) : \mathcal{A}^t \times T \to O$ | The decision function which determines the behavior of agent $a$ at time $t$ |
| $O = \{o_1, ..., o_n\}$ | The set of $n$ possible actions |
| $P_f(a,t,r) : \mathcal{A}^t \times T \times R \to [0, 1]$ | The probability at time $t$ of agent $a$ to forage resources of type $r$ |
| $P_r(a,t) : \mathcal{A}^t \times T \to [0, 1]$ | The probability of reproduction of agent $a$ at time $t$ |
| $C_r$ | The normalization constant of reproduction |
| $P_d(a,t) : \mathcal{A}^t \times T \to [0, 1]$ | The probability of death of agent $a$ at time $t$ |
| $d(a,t) : \mathcal{A}^t \times T \to \mathbb{N}_{0 \leq L}$ | The age function |
| $C_d$ | The normalization constant of death |
| $F^t = \{\phi_{i,r}^t : \phi_{i,r}^t > 0\}$ | Set of all cells containing resources |
| $s_1, s_2 \in [0,1]$ | Discovery rates of resource types 1 and 2 |
| $\gamma \in \mathbb{R}_{>0}$ | The skill compatibility |
| $m \in \mathbb{N}_{\geq 0}$ | The marginal rate of substitution of $s_1$ for $s_2$ |
| $b : T \to \mathbb{R}^n$ | The behavior function which assigns a value to every action |
| $T_{a,t}^i = \{i \in E^t : i \text{ is visible to } a\}$ | The perception vector of agent $a$ at time $t$ |
| $H_{a^t}^t = \sum_{r \in R} H_{a^t,r}$ | The foraging history of agent $a$ at time $t$ |
| $H_{a,r}^t = \sum_{t \geq j \in T_{a,r}} g(a, s_j^a, r)$ | The foraging history of agent $a$ and resource type $r$ at time $t$ |
| $T_{a,r} = \{t \in T : a \text{ chooses to eat } r\}$ | The times at which agent $a$ executes a foraging action on a resource of type $r$ |
| $L \in \mathbb{N}_{>0}$ | The simulation length |
| $l \in \mathbb{N}_{>0}$ | The length of seasons |

Table 1: Mathematical notation in order of appearance in the text.
The fitness function of an agent \( a \in A \) is defined as \( f(a,t) \propto \epsilon \propto (g(a,s^t_a,r), E^t, B(a,t), P_f(a,t,r), s^t_a) \) and is assumed to be directly proportional to the energy gained through foraging, which in turn is proportional to the foraging success.

A roulette wheel algorithm with stochastic acceptance regulates reproduction and death of agents. Agents reproduce asexually with a probability \( P_r(a,t) = f(a,t)/C_r \) proportional to their fitness. The energy level \( \epsilon \) of the parent is then split equally between the parent and the offspring and the offspring inherits a randomly-mutated copy of the parent’s generic configuration. Agents die with a probability \( P_d(a,t) = d(a,t)/C_d \) proportional to their age.

The environment is modeled as a squared grid of size \( m \times m \) with continuous boundary conditions, in which agents move to neighboring cells. The number of cells with resources, \( |F^t| \), is constant at every point in time: whenever one cell is emptied, a random quantity of resources of the same type spawns at a random location. The environment contains two resource types, i.e. \( |R| = 2 \), whose proportion vary over time [20]:

The skill level \( s^t_a \) determines a trade-off between the foraging success of the two resource types: the higher the success rate is for one resource type, the lower it is for the other type. With a direct relation between skill and probability, i.e. \( P_f(a,t) = s^t_a \), the average total intake is equivalent to the average resource distribution: a specialist individual forages with certainty one type of resources but none of the other, while a generalist individual forages each resource with 50% probability. Assuming a non-linear relation between skill level and foraging probability instead, e.g. \( P_f(a,t) = (s^t_a)^3 \), then a specialized strategy leads to higher fitness than a generalist strategy.

The discovery rates of two resource types are constrained by the equality \( s^\gamma_1 + s^\gamma_2 = D^\gamma \), with \( \gamma \) being the skill compatibility, \( s_1, s_2 \geq 0 \) and \( \gamma, D > 0 \) [33]. In this model \( m = (s_2/s_1)^{\gamma-1} \) represent the marginal rate of substitution of \( s_1 \) for \( s_2 \), which determines by how many units the discovery rate of \( s_1 \) must be reduced in order to increase the discovery rate of \( s_2 \) by 1. All the experiments presented in this paper assume \( m = 1 \), i.e. reducing one skill by one unit makes the other skill increase by one unit.

The degree of specialization of the population is measured by the distribution of skill values at each given timestep, normalized by the population size at that timestep.

\[
M^1(v,t) = |\{a \in A^t : s^t_a = v\}|/|A^t|
\]

The foraging history of the population at value \( x \) is measured as the
frequency of agents in the population who, during their lifetime, foraged a specific proportion of type $i$ resources corresponding to $x$.

$$M^2(x, r) = |\{a \in A : H_{a,r}^L / H_a^L = x\}| / |A|$$

Additionally, standard measures of group behavior, taken from [34, Pag. 241], are used to quantify the specialization of the population. The measure are defined and explained in Appendix II.

An agent’s behavior $B(a, t) = \arg \max (b(I_a^t))$ is encoded in its phenotype and associates each perception vector, containing a representation of the surroundings that informs about the presence of resources, to an action.

### I.1 Mathematical model sensitivity to different $q$ values

This section compliments the analytical model introduced in section 4 considering different relationships between the skill level and the foraging success.

The results introduced in section 4 are validated for different relationships between the skill level and the foraging success and in absence of plasticity costs. Figure 10 and Figure 11 show that the same considerations hold also if $q = 1$ and $q < 1$ respectively.

![Figure 9](image_url)

(a) Results for $a_0 = 0.5$. (b) Results for $a_0 = 0.6$.

Figure 9: Adaptation cost $c = 0$ and for $q > 1$. Note that values of $\delta > 0.5$ now maximize the fitness so an evolutionary outcome is possible where a mix of specialists and generalists co-exist.
Figure 10: Fitness for different combinations of skill level and $\delta$ for $q = 1$: intermediate skill levels deliver the same fitness as extreme levels, thus a mixed population will evolve. An intermediate skill level of 0.5 is optimal if $\delta = 0.5$, while an extreme skill level is optimal for high or low values of $\delta$.

Figure 11: Fitness for different combinations of skill level and $\delta$ for $q < 1$: intermediate skill levels deliver higher fitness than extreme levels, hence specialists have always a lower fitness than generalists. An intermediate a skill level is optimal in any circumstances.

I.2 Model assumptions.

The analytical model relies on restrictive macroscopic assumptions which enable a straightforward analysis:

- The fitness of agents is modeled over an abstraction of individual cycles (periods of two seasons that repeat) that removes the time component.
Available resources are assumed to be constant and equal to the average over a cycle.

Agents do not move, instead they access resources of types 0 and 1 with probabilities $a_0$ and $a_1$ respectively.

Evolution is not modeled explicitly, instead the evolutionary outcome is inferred from the fitness levels obtained within each cycle.

Learning is modeled as skill level plasticity: the parameter $\delta$ determines the range of skill levels an agent can choose at the start of the cycle.

## II Diversity measures for social foraging

Assume a group contains $G$ individuals and $S$ discrete resource types.

- $n_{gs}$ is the number of items of resource $s$ consumed by individual $g$.
- $n_g = \sum_{s=1}^{S} n_{gs}$ is the total foraging of individual $g$.
- $n_s = \sum_{g=1}^{G} n_{gs}$ is the number of resources of type $s$ foraged by any agent.
- $n_\cdot = \sum_{g=1}^{G} \sum_{s=1}^{S} n_{gs}$ is the number of resources of any type consumed by any agent.

Each $n_{gs} > 0$ defines a sample proportion $p_{gs}$ where $p_{gs} = n_{gs}/n_\cdot$, which is used to estimate the total, cross-classified diversity:

$$h'(g \times s) = - \sum_{g=1}^{G} \sum_{s=1}^{S} p_{gs} \ln(p_{gs})$$

The following measures [34, Pag. 241] of social foraging are based on the concept of diversity [46]:

- Among-resource diversity: $h'(s) = - \sum_{s=1}^{S} p_s \ln(p_s)$
- Conditional phenotypic diversity within resource $s$: $h'(g|s) = - \sum_{g=1}^{G} \left( \frac{p_{gs}}{p_s} \right) \ln\left( \frac{p_{gs}}{p_s} \right)$
- Average within-resource diversity: $E[h'(g|s)] = \sum_{s=1}^{S} p_s h'(g|s)$
- Among-individual diversity: $h'(g) = - \sum_{g=1}^{G} p_g \ln(p_g)$
- Conditional resource-consumption diversity: $h'(s|g) = - \sum_{s=1}^{S} \left( \frac{p_{gs}}{p_g} \right) \ln\left( \frac{p_{gs}}{p_g} \right)$
- $E[h'(s|g)] = \sum_{g=1}^{G} p_g h'(s|g)$
A generalized diet includes most of all resources types in roughly equal proportions. A specialized diet includes one or a few resource types at high proportions, and very low proportional levels of the remaining resources. The group’s diet refers to the pooled resource consumption of all group members.

- Among-resource diversity $h'(s) = -\sum_{s=1}^{S} p_s \ln(p_s)$
  - Low: group specializes because individuals have similar specialized diets
  - High: group generalizes, individuals may generalize or different individuals have different specialized diets.

- Average within resource diversity $E[h'(g|s)]$.
  - Low: different individuals have different specialized diets, so group generalizes; similar effect occurs whenever different individuals consume different total amounts of food.
  - High: individuals have similar diets, whether generalized or similarly specialized, group diet may then be generalized or specialized.

- Among-individual diversity $h'(g)$.
  - Low: individuals differ in amount of food consumed, independently of each individual’s specialization or generalization.
  - High: Individuals consume similar amounts of food, independently of each individual’s specialization or generalization.

- Average within-individual diversity $E[h'(s|g)]$.
  - Low: Individuals specialize independently, group may consequently specialize or generalize.
  - High: individuals generalize, group consequently generalizes.

Figure 12: Diversity measures for social foraging. Reproduced from [34, Pag. 241]
III Experimental setting

This section describes the experimental setup used to highlight the different effects of learning in evolution.

Experiments consist of a population of agents foraging under the effect of natural selection. Agents are located in a $20 \times 20$ grid with periodic boundary conditions. Each patch contains a random number of resource units smaller than 5. Each season has a resource type associated with it, so for the duration of the season, i.e. 50 time steps, only one type of resource can be found in the environment.

The first computational experiment compares the speed of different types of learning. In this case the evolutionary component of the simulation is disabled as changes in the genetic configuration are not relevant. The second experiment replicates previous results in the literature by showing the existence of the Baldwin effect (expediting and delaying) in the dynamic foraging environment. The third experiment compares the genetic adaptation of two populations, one of reactive agents and one of learning agents, in a fast-changing seasonal environment and shows the Baldwin veering effect.
III.1 Parameters of the model

| Parameter       | Value | Description                                                                 |
|-----------------|-------|-----------------------------------------------------------------------------|
| **Initialization** |       |                                                                             |
| num-agents      | 100   | The size of the initial population.                                         |
| skill-level     | 0.7   | The average skill level of the initial population.                          |
| **Environment** |       |                                                                             |
| field-size      | 20    | The size of the grid.                                                       |
| max-food        | 50    | The maximum food quantity that a cell can contain.                          |
| num-food        | 400   | The number of cells containing some food.                                   |
| food-proportion | 1.0   | The proportion of the 'seasonal' food with respect to the total amount of food. |
| food-energy     | 10    | The energy given by a unit of food.                                         |
| **Agent**       |       |                                                                             |
| max-age         | 5000  | Age after which the probability of death is 1.                              |
| max-energy      | max-age | Age energy after which the probability of reproduction is 1.                |
| fov-radius      | 3     | How far agents can perceive.                                                |
| **Simulation**  |       |                                                                             |
| sim-length      | 5001  | The length of the simulation.                                               |
| max-agents      | 2000  | The maximum population size, enforced by killing random agents in surplus. |
| samples         | 50    | The number of independent simulations.                                      |

Table 2: Description of the parameters in the model and their value.

III.2 Learning

This section discusses how different learning algorithms behave when faced with a variable environment, in terms of convergence and adaptation to change. Different learning algorithms are compared:

- PQL: Reinforcement learning using a single layer feed forward perceptron as its network architecture to "store" and query the Q-values
- RQL: Reinforcement learning using a variation of a Restricted Boltzmann machine [44] for the network architecture
- Q-Learning [43]
• Deep Reinforcement Learning [45]: using 3 fully connected layers, \((\text{perception}_\text{size} \times \text{perception}_\text{size} \times 5), (\text{perception}_\text{size} \times 5 \times \text{number}_\text{of}_\text{actions} \times 5), (\text{perception}_\text{size} \times 5 \times \text{number}_\text{of}_\text{actions})\)

using gradient descent and action replay with a memory replay of 50 experiences.

The results of each learning algorithm are the average of 300 independent simulations, parameters are consistent across simulations.

Results show that different types of learning algorithm have different speeds of convergence (cf. Figure 13) shows the proportion of agents choosing to eat while a specific type of food is in their foraging range. Some learning algorithms adapt faster than others to changes in the environment.

RQL is the fastest to adapt to a change in the environment, and it also shows a stronger tendency to forget the learned behavior in the opposite season. DRL is the slowest to learn. This is not surprising as deep networks are generally trained with large datasets and used for much more complex tasks.
Figure 13: Comparison of different learning algorithms. Each graph represents the frequency over time of an agent choosing to forage each resource type whenever the corresponding resource is available. A higher value produces a higher fitness, assuming the corresponding resource is available in the environment. Each curve is the average of 300 independent simulations. Season length is 3000 and all simulations start in the same season.

III.3 The Baldwin Veering Effect and the learning algorithm

This section analyses further the effect of different learning algorithms.

In order to analyze the consistency of the results in respect to the type of learning, experiments have been replicated with different learning algorithms (Figure 14).
Figure 14: The genetic configuration evolved with different learning algorithms. All tested algorithms produce qualitatively similar results.

As the different algorithms produce quantitatively similar results, RQL has been chosen as the learning algorithm in the experiments shown in section