Why learn? The adaptive value of associative learning in wild populations

Julie Morand-Ferron

The ability to associatively learn is highly conserved, having been evidenced in all bilateral animals tested to date. This general cognitive process has been shown to play a role in a wide diversity of behaviours, including interactions with predators, prey, rivals and mates. Learning is thus expected to be essential for survival and reproduction in many species, but because of associated costs, it is also predicted to be fine-tuned to prevailing conditions by selective processes. Considering the importance of learning in determining populations' response to environmental changes as well as potential impacts on evolutionary rates, there is still a paucity of evolutionary studies on learning, especially in natural populations. Here I review recent progress in our understanding of the evolutionary causes and consequences of intra-specific variation in associative learning abilities in wild populations, and discuss areas for further investigation.

Address
Department of Biology, University of Ottawa, 30 Marie Curie, Gendron Hall 160, Ottawa, ON K1N 6N5, Canada

Corresponding author: Morand-Ferron, Julie (jmf@uottawa.ca)

Introduction

The ability to learn is highly conserved among animals. Even simple animals such as nematodes can learn associations between cues and behavioural responses, or between two cues [1,2]. The phylogenetic distribution of associative learning points to the early Cambrian period for its appearance, when the ability to predict the behaviour of predators, prey, and competitors may have provided an evolutionary advantage over systems lacking such an ability [3]. Since this evolutionary innovation, learning capabilities seem to have diversified widely, as evidenced by large inter-specific differences in learning speed in associative tasks (e.g. [4,5]), and in the

probability that a given association is learned ('prepared learning', reviewed in Ref. [6]).

Several evolutionary hypotheses have been proposed to account for this diversity, but the extent to which various sources of selection are responsible for inter or intra-specific variation in learning abilities is still not well understood. Moreover, we still lack direct empirical evidence for the action of natural or sexual selection on learning abilities in natural populations. Recent progress has however been made in quantifying individual variation in learning abilities in a variety of species, and in examining causes and consequences of this variation. Here I review recent studies on associative learning performance in wild populations pertaining to: (i) individual variation and heritability; (ii) links with fitness; and (iii) agents of selection. I invite readers interested in the adaptive significance of learning to also consult the rich literature on more specialised forms of learning and memory (*e.g.* spatial memory and imprinting [7,8]), social learning [9,10], as well as learning in the context of sexual selection (reviewed by Ref. [11], see also Ref. [12]).

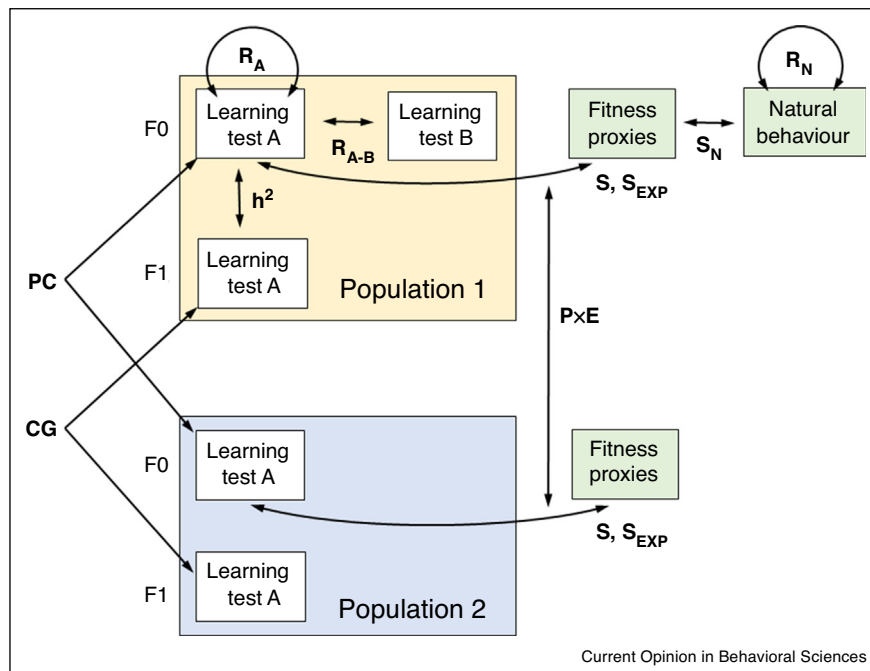## Heritability and individual variation in learning

Associative learning has long held a prominent place in evolutionary biology studies targeting cognitive traits. In particular, the contribution of inheritance to variation in learning abilities has been examined through numerous artificial selection experiments (*e.g.* [13]) and/or measurements of heritability on learning performance (*e.g.* parent–offspring regression [14], proportion of variance accounted for by natal nest [15••]). In a recent review, Croston *et al.* [16••] reported heritability values for learning abilities mostly ranging between 0.3 and 0.5 (*e.g.* $h^2 = 0.37$: realized heritability of fear conditioning in *Mus musculus* [17]; $h^2 = 0.39$–0.54: ability to learn in *Apis mellifera* [18]). Along with evidence for rapid responses to artificial and experimental selection on learning ability (reviewed in Refs. [19,20]), these moderate heritability measurements underline the evolutionary potential of traits related to associative learning processes (see also Ref. [21••]). It is noteworthy that none of the heritability values reported in Croston *et al.* [16••] are from natural populations exposed to ecologically-relevant, complex environments (but see Ref. [22] for heritability estimates on problem-solving success in wild great tits, *Parus major*). Although there is no heritability estimate for associatively-learned behaviour from wild populations, researchers often quantify individual variation in

wild-caught animals, for instance in hypothesis tests of correlates of learning performance (*e.g.* personality [23]). While values for individual performance in learning tests have been found to range widely, it is not clear to what extent these measurements capture repeatable aspects of learning performance, because each learning task is usually conducted only once with each subject ([24]; but see Ref. [25]). As a consequence, the repeatability of learning performance (and that of other cognitive traits), is yet to be estimated for most populations.

Measuring the repeatability of the speed at which new associations can be learned (Figure 1: R_{A-B}) is challenging, as once learned, a new association is not novel anymore. A different association has to be presented, on the assumption that stimuli are different enough not to elicit generalization, and that the same cognitive processes are targeted. An alternative is to assess repeatability of individual performance within a task; as learning is necessarily measured over multiple trials, useful estimates of between- and within-individual variation can be extracted from learning datasets (Figure 1: R_A). Analytic treatments of learning datasets have often relied on aggregate values (*e.g.* proportion of correct choices per block of 10 trials, number of trials to criterion) or point estimates (*e.g.* maximum slope of accuracy over trials) to characterize individual learning performance. However, mixed-models and random regressions could be used to quantify and compare individual rates of learning, and to estimate within-task repeatability in learning parameters. For instance, wild great tits (*Parus major*) have been found to differ significantly: (i) in individual slopes for colour choice accuracy over successive trials (random slope: trial x ID), suggesting individuals learned this association at different rates [26]; and (ii) in individual intercepts for choice accuracy (random intercept: ID) in a serial spatial reversal task, suggesting that some individuals consistently returned more correct choices than others throughout the reversals

Figure 1

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Schematic representation of approaches to examine the causes and consequences of individual variation in learning abilities. Each box represents a natural population, with individuals from the current generation (F0) and their offspring (F1). Quantifying individual variation in two different learning tests A and B allows examining R_{A-B}, the repeatability of learning speed (*e.g.* trials to criterion) or accuracy (*e.g.* proportion of correct choices). Multi-trials learning datasets also allow estimating consistency of individual differences in performance within a learning test A, R_A. Quantifying individual variation in F0 and F1 on learning test A, or in individuals of known relatedness in F1 allows determining heritability (h^2) of learning performance. Hypotheses on agents of selection for learning can be tested by comparing learning performance in individuals from two, or ideally, more than two populations exposed to different environments (PC). The contribution of local adaptation to population differences can be examined using a common garden approach (CG). Natural variation in individual learning performance can be examined against fitness components to quantify selection (S) on the trait studied, and experiments can be used to examine the adaptive value of learned information (S_{EXP}). A priori predictions can be made on the direction and strength of selection, for instance if the rate of change in a given agent of selection is known in the population, or by comparing two populations (P × E) that differ in environmental states determining the costs and benefits to learned behaviour. Finally, the rate of improvement in natural behaviours can be examined against fitness (S_N) using long-term individual tracking; phenotypic variation can be partitioned between- and within-individuals (R_N).