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# The evolutionary relevance of social learning and transmission of behaviors in non-social arthropods

Caroline M. Nieberding <sup>1\*</sup>, Matteo Marcantonio <sup>1</sup>, Raluca Voda <sup>1</sup>, Thomas Enriquez <sup>2</sup> and Bertanne Visser <sup>2</sup>

<sup>1</sup> Evolutionary Ecology and Genetics group, Earth and Life Institute, UCLouvain, Louvain-la-Neuve, Belgium; caroline.nieberding@uclouvain.be

<sup>2</sup> Evolution and Ecophysiology group, Earth and Life Institute, UCLouvain, Louvain-la-Neuve, Belgium; bertanne.visser@uclouvain.be

\* Correspondence: caroline.nieberding@uclouvain.be

**Abstract:** Research on social learning has centered around vertebrates, but evidence is accumulating that small-brained, non-social arthropods also learn from others. Social learning can lead to social inheritance when socially acquired behaviors are transmitted to subsequent generations. Here, we first highlight the complementarities between social and classical genetic inheritance, using oviposition site selection, a behavior critical for many non-social arthropods, as a hypothetical example. We then discuss the relevance of studying social learning and transmission in non-social arthropods and document known cases in the literature, including examples of social learning from con and hetero-specifics. We subsequently highlight under which conditions social learning can be adaptive or not. We conclude that non-social arthropods and the study of oviposition behavior offer unparalleled opportunities to increase our understanding of social learning and inheritance.

**Keywords:** Behavioral plasticity; Communication; Culture; *Drosophila*; Fitness; Herbivores; Oviposition site selection; Natural selection; Traditions

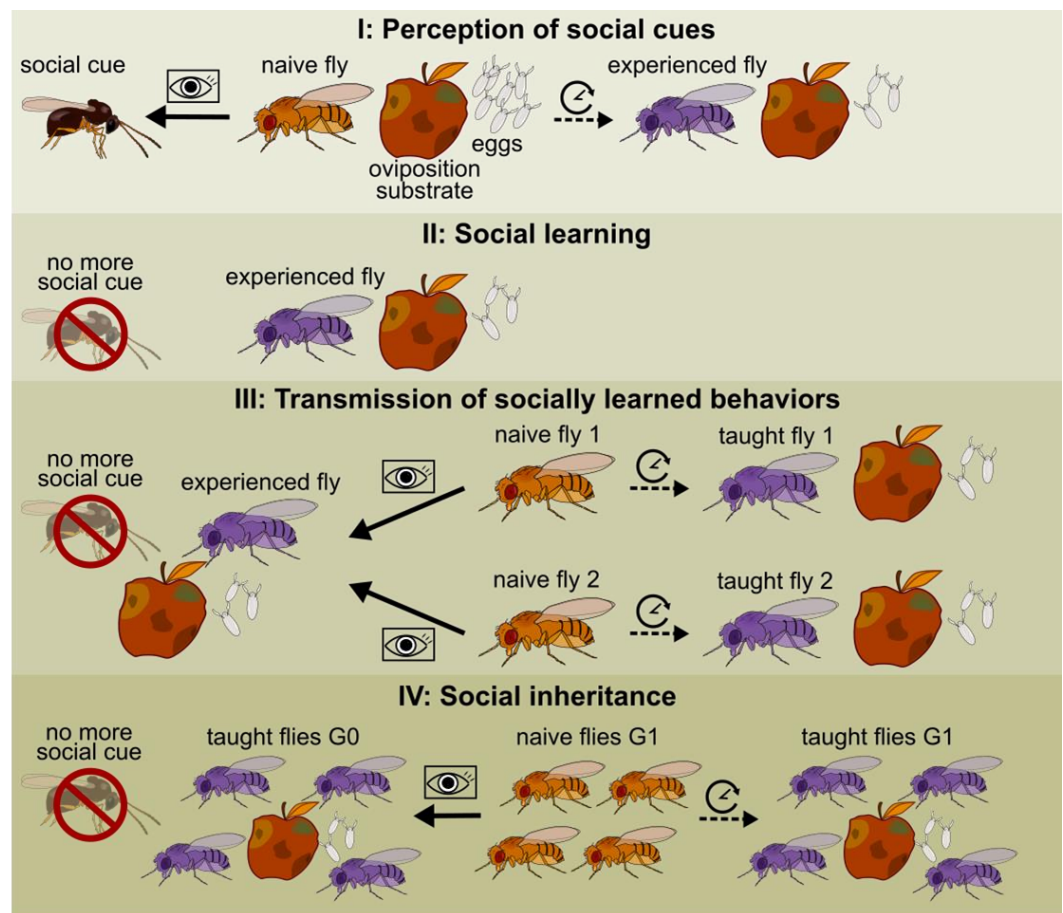
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## 1. Introduction

The emergence and spread of novel behaviors through **social learning**, or “learning from others”, has been documented in a wide variety of animals, mainly in social vertebrates [1–5]. In recent years, social learning has been demonstrated to act as the “second inheritance system”, that functions in parallel with classic genetic inheritance, called “**social inheritance**”, in a number of social vertebrates in the wild. Social inheritance entails the perception of behaviors performed by others that are subsequently taken over (e.g., by imitation, imprinting or teaching) and spread throughout a population and subsequent generations [6–9](see Figure 1 depicting the steps leading to social inheritance). Aside from human cultural evolution, famous examples include the transmission of tool use in apes, and song communication in social whales and birds [8,10–14].

Social vertebrates have been at the forefront of research on social learning, but studies using small-brained and short-lived social invertebrates are increasing in numbers. In an exceptional experiment with *Bombus terrestris* bumblebees, Alem et al [15] showed that some individuals can innovate by acquiring a non-natural, novel behavior for feeding: string pulling. Once this novel behavior was observed by others, naïve bees learned how to perform string pulling themselves. The authors further showed that string pulling behavior could spread from a single knowledgeable individual to many other bees, even when the original demonstrators were no longer present (completing steps 1 to 4 in Figure 1; [15,16]). For invertebrates, most work has been done with social insects and recent findings support the idea that insects have the cognitive abilities necessary for transmission of socially learned behaviors [17–20].

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**Figure 1: The steps involved in social inheritance.** Step I cue perception: Individual 1 perceives a **social cue**, e.g., the presence of a parasitic wasp that can parasitize and kill the larvae of *Drosophila melanogaster* (based on Kacsoh et al 2015 eLife). In response to the **social cue**, individual 1 changes its behavior, e.g., female *D. melanogaster* reduce oviposition (fewer eggs are laid). Step II, **social learning**: Individual 1 has learned about the **social cue** and is now **experienced**, meaning that the behavioral adjustment is copied and continues even when the **social cue(s)** are no longer present, e.g., *Drosophila* females continue laying fewer eggs even when the wasp and the original experienced fly demonstrator are no longer present. Step III, transmission: The socially learned behavior is **taught** by individual 1 to a **naive** individual 2 (i.e., through visual and olfactory cues) that then changes its behavior, e.g., a **naive** *Drosophila* female changes her oviposition behavior after learning from an **experienced** female that lays fewer eggs after exposure to a parasitic wasp. Step IV, **social inheritance**: The socially learned behavior spreads throughout the population and over subsequent generations, e.g., other *Drosophila* females (including those belonging to other species) perceive the behavioral change of individual 1 or 2 and subsequently reduce their egg numbers (based on Kacsoh et al 2018 PLoS Genet). For **social inheritance**, **naive** individuals belonging to the next generation should acquire behaviors from **experienced** females exhibiting socially learned behaviors. This remains to be tested explicitly in the example of **social learning** of wasp threats in *Drosophila*. Of note: there is a large array of social cues (olfactory, visual, olfactory, etc...), from conspecifics, hetero-specifics, or both, as well as many mechanisms of social learning (conditioning, copying, associative learning etc...) that all have the potential to lead to **social inheritance**.

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In this perspective, we aim to provide a synthesis of the existing literature on **social learning** in non-social arthropods and why studying non-social arthropods is both relevant and timely. While learning of foraging and host finding behaviors have been discussed elsewhere [21,22], here we illustrate the complementarities between genetic and social heredity using the hypothetical example of social transmission of oviposition site selection. Oviposition site selection is a behavioral trait of key ecological significance for the relationship between organisms and their habitat, as the decision on where to lay eggs can have massive consequences for fitness and demography ([23] and refs therein). This is particularly true for herbivorous insects with limited mobility as juveniles, because the egg-laying site is often also the offspring's food source. The moment oviposition takes place is the time that colonization of new suitable habitats occurs at the level of populations ([23] and refs therein). There is ample evidence for **non-social learning** (i.e., learning solely from previous experience, or "autonomous" learning) for oviposition in

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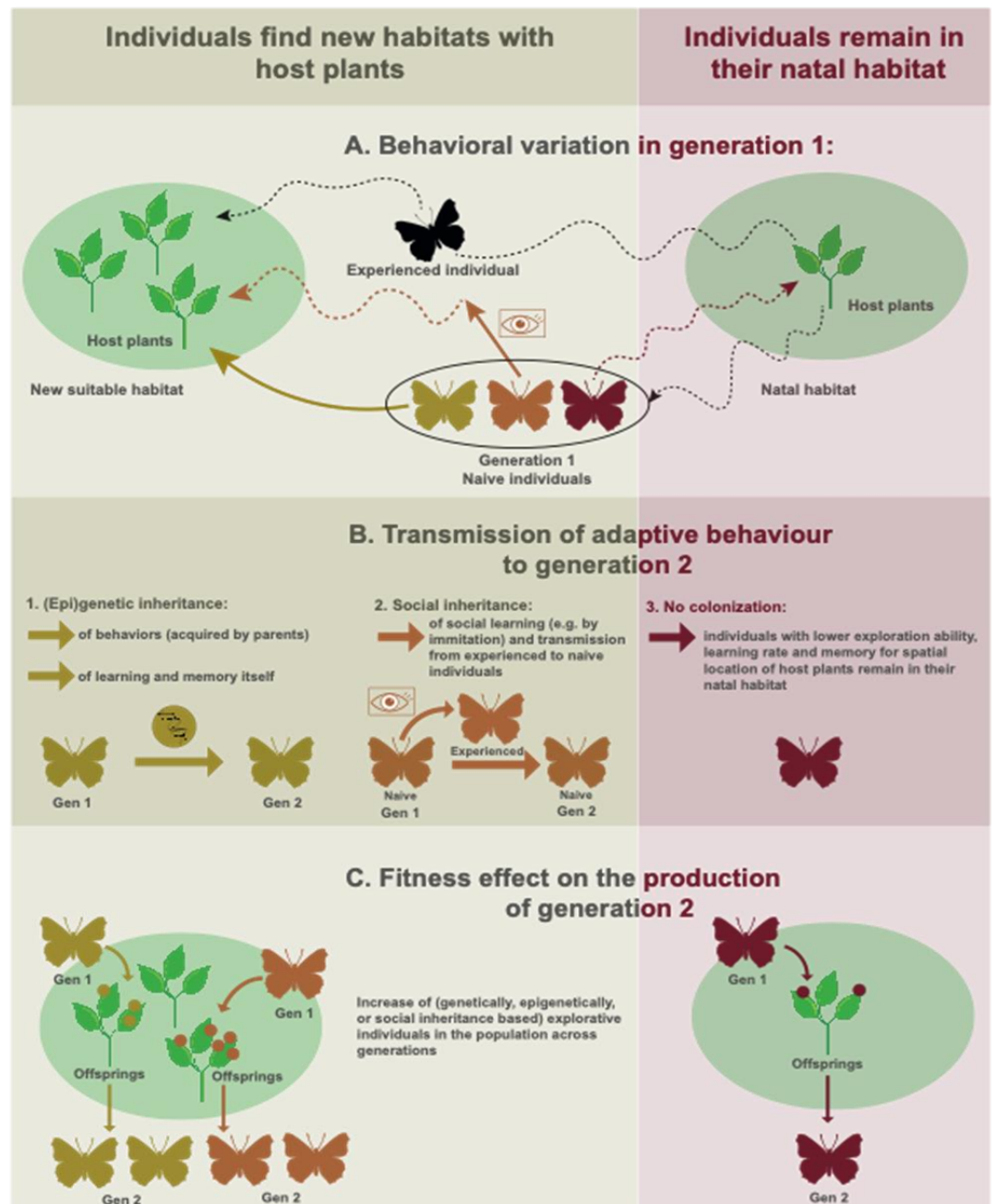
wasps, flies, moths and butterflies (e.g., [24–32]), but **social learning** for oviposition is reported by an increasing number of studies (Table 1). We extend our discussion to cases where social learning occurs not only from interactions between conspecifics, but also from hetero-specifics, and to other types of behavior. We are paying particular attention to the evidence for, and quantification of, the adaptive value of social learning using existing empirical evidence for fitness effects.

## 2. Genetics, epigenetics and social inheritance in the context of oviposition site selection

There are two non-mutually exclusive mechanisms by which socially learned behaviors can be transmitted to successive generations in a population. In his review, Whiten [7] puts forth the parallels between genetic and social inheritance, where the former encompasses genetic changes that spread throughout populations, and the latter pertains to the spread of socially learned behaviors over generations [8]. Genetic or epigenetic inheritance is based on DNA, RNA or protein materials present in the parental germ cells that are passed to the offspring when zygotes are formed. Social inheritance is transmitted independently from the germ line material, by perception and acquisition of behaviors between individuals belonging to successive generations. Genetic and social inheritance can thus function alone or interact and act simultaneously ([33–36]; see Figure 2 using oviposition site selection as an example).

There is evidence that most behaviors and behavioral variation between individuals have some genetic basis [37–41]. For example, several candidate loci were identified and associated with phenotypic variation for memorizing locations in the fly *Drosophila melanogaster* [42]. The identification of candidate loci paves the way for finding the genetic basis of complex behavioral traits, including spatial exploration ability (e.g., spatial learning rate) and memory retention of spatial location (e.g., suitable resources, including host plants for oviposition). Genetic variants with higher learning rate and memory retention may thus become more numerous in successive generations, when there is positive selection for oviposition site selection (Figure 2). There is further evidence that learning ability itself has a genetic basis and that there is genetic variation in learning ability between individuals in various invertebrate, non-social taxa (reviewed in [42–46]). One gene whose allelic variation and expression is associated with differential learning rate and memory retention is the *foraging* gene (“*for*”), a pleiotropic gene that produces a cyclic GMP-dependent protein kinase (PKG), the protein of which is involved in energy homeostasis [47–50]. Although the exact function of *for* in learning (and social learning) remains to be understood [51], the existence of genetic variation for learning ability suggests that genetically “better” learners will proportionally increase in subsequent generations, for example if social learning of oviposition site selection from conspecifics is locally adaptive.

For epigenetic inheritance, behaviors can also be acquired by parents and transmitted epigenetically to offspring, as was found for multiple behaviors and species [52–54]. For example, mice exposed to a neutral fruity odor while receiving a mild electric shock adopt a startle behavior later in life while only experiencing the odor, a behavior that is subsequently passed on to their children and grandchildren when sensing the odor without the shock [55,56]. These results pointed to the fixation of



**Figure 2: (Epi)genetic and social inheritance for oviposition site selection can affect the colonization of new suitable habitats with better host plant resources.** **A:** Variation between individuals in oviposition on host plants can be due either to (epi)genetic variation (1) or variation in **social learning** skills (2). **Social learning** can lead to the colonization of new suitable habitats by **naive** individuals, for example by following **experienced** individuals towards a new habitat patch. Here, **social learning** is based on imitation and can occur through **horizontal**, **oblique** or (more rarely so) **vertical transmission**. Individuals not relying on **social learning** from conspecifics have a lower probability of finding new suitable habitats for oviposition (3). **B:** More adaptive behavioral variants for finding a new suitable habitat for oviposition can be transmitted through genetic or epigenetic variants. In addition, social learners outperform individuals not using **social cues** to learn about resource distribution in their environment. Transmission of **social learning** ability from parents to offspring can be genetically based or epigenetically transmitted (yellow arrows), but in addition **social inheritance** allows younger individuals to locate new habitats based on social information provided by older conspecifics (orange arrows). **C:** The increasing ability of individuals within a population to learn and remember the spatial location of resources, such as host plants for oviposition, can be due to selection of (epi)genetic variants of the adaptive behavior, including learning rate and memory retention, or to social transmission of the spatial location of resources from older to younger individuals leading to **social inheritance**. The accumulation of advantageous modifications of behavior in populations across generations may produce differential local adaptation between populations in socially learned traits, based on local environmental conditions and geography in much the same way as local adaptation through genetic differentiation does.

epigenetic variation affecting the expression of olfactory genes [55]. In another study, mice separated from their mothers during early life showed depression-like behaviors and changes to the metabolism of adult male mice (as a result of small RNAs acting on sperm and the brain), that were subsequently passed on to their own offspring [52]. In an invertebrate, naïve *C. elegans* nematodes were first attracted to lethal pathogenic bacteria, but then learned to avoid exposure. This behavior was found to persist up to four generations and was related to small RNA expression in neurons [57–59]. There is, to the best of our knowledge, no evidence yet for epigenetic transmission of spatial localization and memory of suitable resources, as depicted in our example of Figure 2, nor for other behaviors typically related to oviposition site selection in insects, such as transmission of preference for novel specific host plant species across generations [56,60]. It will be important to tease apart the contribution of the genome, epigenome, and social inheritance (described below), to understand how insects track and potentially adapt to rarefying suitable habitats through oviposition site selection behavior [61].

The second main inheritance mechanism, social inheritance, is based on social learning of behaviors between interacting individuals, such that learned behaviors can also be propagated without a genetic or epigenetic material basis across generations, producing basic **traditions** and **culture** (Figures 1 and 2). Traditions and culture have so far mainly been observed in social vertebrates and more recently in social insects (e.g., [15]). Social learning can increase local adaptation of individuals relying on socially acquired information by increasing their chance, or reducing the time or energetic cost these individuals need to find and remember the location of a resource, such as host plants for oviposition in a new suitable habitat (i.e., oviposition site selection; Figure 2A,B). Social learners may thus have overall quicker and/or more access to suitable resources for survival and reproduction compared to conspecifics that are not using or remembering social information. This, in turn, may lead to increased reliance on social information across generations (Figure 2C), whether socially acquired traits are transmitted over longer evolutionary times and multiple generations by **culture** or not.

Two key aspects of social inheritance now need to be examined and tested both in the laboratory and in the wild. First, it will be important to quantify to what extent social inheritance is more than a singularity in the diversity of evolving life, compared to genetic inheritance (all living species have DNA or RNA and cell division), including in non-social animals. Second, quantifying the adaptive value of social learning is of central importance (as depicted in steps A and B of Figure 2), whether socially acquired traits are transmitted over longer evolutionary times by traditions or some form of culture, or not.

### 3. Relevance of social inheritance in non-social arthropods

Socially acquired behaviors produce social inheritance only if they are transmitted over longer evolutionary times, hence multiple generations, leading to **traditions** and/or **culture**. It is now timely to examine the extent of the transmission of socially acquired behaviors as an important second inheritance system in nature (step 4 in Figure 1, Figure 2C), also in small-brained non-social invertebrates that make up at least half of the species diversity on Earth [62,63]. The transmission of socially acquired behaviors across generations requires that individuals of different life stages or age groups live in contact with each other (Figure 1). Many insects indeed have overlapping generations, where individuals belonging to different generations co-occur [64]. Furthermore, eusocial species have, by definition, overlapping generations, but multiple additional insect taxa have social structures allowing the transmission of socially acquired behaviors over generations, through maternal, paternal and biparental care [65–67]. Maternal and biparental care takes the form of egg and/or offspring guarding, defense, nidification, and/or feeding facilitation or progressive provisioning and underpins the single most widespread form of sociality found in “non-eusocial” insects. These behaviors have been reported for >40 insect families belonging to 12 orders, as well as several non-insect

arthropod groups, such as spiders, scorpions, opiliones, mites, chilopodes and amphipod crustaceans [65]. Moreover, in a diverse array of mainly hemimetabolous arthropods, including treehoppers, true bugs (Heteroptera), thrips, cockroaches and social spiders [68], mixed supercolonies of adults and immatures are found. While historically **traditions** and **cultures** have not actively been looked for in most insect taxa to date, the social structure of many insect species provides opportunities for transmission and inheritance of socially acquired behaviors far beyond the few documented cases in well-known, emblematic, social insects.

#### 4. Social learning of oviposition behavior and social learning from hetero-specifics

Choosing an optimal substrate for oviposition is critical for offspring survival and fitness, and social learning can help individuals to adjust and optimize egg laying decisions. *Drosophila* sp have been a popular model system for studying oviposition behavior [69–72]. For example, adult females learn to interpret and use a wide variety of cues from conspecifics at different life stages when choosing an oviposition site. Visual cues, such as the presence of conspecific eggs and/or larvae on oviposition substrates [70,71], interactions with more experienced female demonstrators [71], as well olfactory and even auditory cues produced by conspecifics [73,74] have been shown to positively influence the decision of females for oviposition. This implies that the benefits of conspecific attraction in oviposition site selection may outweigh the costs of competition in the wild [74,75]. In the context of research on social learning in *Drosophila*, the large knowledge-base on cues associated with oviposition site selection, as well as the documented evidence for social learning (Table 1), make it an excellent model for testing whether social learning of oviposition sites can be inherited. Moreover, several other species were found to perceive and act upon social cues, including lepidopterans, hymenopterans, coleopterans and spider mites (Table 1), offering opportunities to investigate social learning, transmission and inheritance of oviposition site selection, also in other systems.

Many examples of social learning focus on interactions between conspecifics, but acquiring social information from other species can also be an efficient way to increase fitness. This is particularly true for non-social insects with limited access to information from conspecifics (such as for early dispersers, insects with small population sizes, and/or species with low conspecific encounter rates (e.g., [76]). Hetero-specifics as a source of information can help to minimize potentially costly errors, such as wasting energy and gametes by mating with the wrong species, but can also be used to decrease predation risk or to locate food sources [77–80]. Social information from hetero-specifics is ubiquitous, but can be challenging to decode and lead to confusion, for example because the cue may have had a different original meaning or purpose than what is interpreted by the receiving species [81,82]. Despite the potential importance of social learning from hetero-specifics, only a handful of studies have investigated it, including in solitary bees [76], parasitic wasps often without assessing potential fitness effects (Table 1).

The value of social information from hetero-specifics has occasionally been studied in non-social insects, such as in the context of increasing oviposition success in *Drosophila* species [83]. Adult *Drosophila* flies can exchange complex information through a combination of visual, olfactory and tactile cues. The divergence in cues that evolved between different species led to the formation of species-specific communication patterns (often referred to as “dialects”). The magnitude of divergence in species-specific communication patterns was found to be correlated to the phylogenetic distance between species. Kacsoh and co-authors [83] exploited this system to test if the degree of hetero-specific social information transfer between *Drosophila* species was related to their relative phylogenetic distance, meaning that phylogenetically close species are more successful in sharing social information. Similar to the experiments described earlier from Kacsoh [84], here *Drosophila* females were presented with visual cues of parasitic wasps that leads to a

Table 1: List of non-social arthropod studies where social cue perception, social learning and transmission of socially learned behaviors was studied (singly or in combination). The table includes column reporting the type of cue and behavior, con (c) or hetero (h) specific learning, whether fitness was tested in the study, and the expected adaptive value of the learned behavior. The steps towards social inheritance refer to those presented in Figure 1.

Species	Cue	Behaviour	Learning from con (c) or hetero (h)-specifics	Steps towards social inheritance	Fitness tested (y/n)	Expected adaptive value	Ref
<b>Oviposition</b>							
<i>Anastrepha ludens</i> , <i>A. obliqua</i> , <i>A. serpentina</i>	Host marking cues	Site selection	c + h	1	n	Decreased larval competition for food	[85]
<i>Drosophila</i> spp	Parasitoid presence (i.e., threat to offspring survival)	Clutch size	c + h	1-3	y	Lower egg predation risk	[83]
<i>D. melanogaster</i>	Auditory tone at 250 Hz	Site selection	c	1, 2	n	Higher survival + offspring protection	[73]
<i>D. melanogaster</i>	Site marking	Site copying	c + h	1, 2	n	Context-dependent: Experiment 1: potential lower parasitism of offspring (dilution) Experiment 2: unclear	[75]
<i>D. melanogaster</i>	Mated females	Site selection	c	1, 2	y	Safer oviposition site	[86]
<i>D. melanogaster</i>	Adult females	Site selection	c	1, 2	n	Offspring survival	[71]
<i>D. melanogaster</i>	Adult females + environmental cues (flavored media, eggs, aggregation pheromone)	Site selection	c	1, 2	n	Offspring survival	[70]
<i>D. melanogaster</i>	Oviposition site markings	Site selection	c	1, 2	n	Offspring survival	[72]
<i>D. melanogaster</i>	Parasitoid presence (i.e., threat to offspring survival)	Clutch size	c	1-3	y	Lower egg predation risk	[84]
<i>D. suzukii</i>	Site marking	Site selection	c	1, 2	n	Reduced offspring competition	[74]
<i>Rhagoletis mendax</i>	Marking pheromones	Host selection	h	1	n	Reduced misallocation of eggs and time spent examining occupied host	[87]
<i>R. suavis</i>	Reproductive status of conspecifics	Egg maturation and development	c	1	n	Faster egg maturation and laying	[88]
<i>Leptopilina boulardi</i>	Oviposition site	Host selection	h	1, 2	n	Offspring survival	[89]

markings							
<i>Necremmus tutae</i>	Host marking cues	Host selection	h	1, 2	n	Exploitation of a new host	[90]
<i>Osmia sp. *</i>	Nest site parasitism	Nest site selection	h	1	n	Enhanced clutch survival	[76]
<i>Sycopaga fusca</i>	Ovipositing site/conspicuous abundance	Site selection	c + h	1	y	Maximized food resource quality, diluted predation	[91]
<i>Trichogramma evanescens</i>	Host + host eggs	Phoresy to oviposition substrate	h	1, 2	n	Efficient and flexible oviposition substrate location	[92]
<i>Danaus plexippus</i>	Ovipositing plant/caterpillar presence	Host plant selection	c	1	y	Lower competition for food resources	[93]
<i>Ephestia kuehniella</i>	Larval pheromone	Clutch size	c	1	n	Reduced larval competition	[94]
<i>Callosobruchus chinensis</i>	Eggs and food resource	Site selection	c	1	n	Maximised food availability for clutch	[95]
<i>Phratora vulgatissima</i>	Conspicuous females	Site selection	c	1, 2	y	Enhanced substrate suitability for clutch	[96]
<i>Tetranychus urticae, T. kanzawai</i>	Eggs + predators	Site selection (leaf surface vs web)	h	1, 2	n	Enhanced clutch survival (predation avoidance or dilution)	[97]
Mating							
<i>D. melanogaster</i>	Mated and virgin females; odors paired with shock stimulus	Courtship (by males)	c	1, 2	n	Increased reproductive success	[98]
<i>D. melanogaster</i>	Adult females and males	Phenotype copying (by females)	c	1, 2	n	Choice for higher quality mates	[99]
<i>D. melanogaster</i>	Mating partner	Phenotype fidelity (by females)	c	1-4	n	No adaptive value	[100]
<i>D. persimilis, D. pseudoobscura</i>	Hetero-specific phenotype	Mating avoidance (by males)	h	1, 2	n	Maximized investment in gametes	[77]
<i>Nasonia vitripennis, N. longicornis</i>	Courtship	Mating avoidance (by females)	c + h	1, 2	n	Maximized investment in gametes	[78]
<i>Bicyclus anynana</i>	Mating partner	Phenotype fidelity (by females)	c	1, 2	n	Higher gamete quality	[101]
<i>Calopteryx splendens, C. virgo *</i>	Wing patch size	Mating preference (by females)	c + h	1, 2	n	Mating with bigger males (proxy for more oxygenated oviposition site)	[102]
<i>Diaphorina citri</i>	Mating partner	Partner location efficiency (by	c	1, 2	n	Maximized energy investment in mate-finding	[103]



males)						
Other						
<i>D. melanogaster</i>	Spatial cues and/or adult conspecifics	Spatial navigation	c	1, 2	n	Better orientation in changing environments [104]
<i>D. melanogaster</i>	Conspecific larvae	Food patch choice	c	1,2	n	Increased offspring survival [105]
<i>Lucilia sericata</i>	Feeding, predator	Avoidance/ attractiveness to food	c + h	1, 2	n	Enhanced survival and maximized food location [80]
<i>Agrotis ipsilon</i>	Pheromones	Gustatory response to sex pheromone	c + h	1, 2	n	Increased reproductive success and food location [79]
<i>Gryllus bimaculatus</i>	Alive and dead conspecifics	Drinking water or saltwater associated with an odour.	c	1, 2	n	Increased survival [106]
<i>Nemobius sylvestris</i>	Indirect predator cues	Predator avoidance	c + h	1, 2	n	Higher probability of survival in the presence of predators [107]
<i>Locusta migratoria migratorioides, Schistocerca gregaria</i>	Conspecific larvae	Propensity to sociality	c	1	n	Local environmental advantages of social or non-social behaviour [108]
*Field conditions						

reduction in the number of eggs laid. When the teacher belonged to a different species, Kacsoh et al [83] observed the same decrease in oviposition. However, while closely related *Drosophila* species were able to efficiently communicate, species that were phylogenetically more distant had limited or no communication abilities. Interestingly, cohabitation in multi-species communities enhanced communication between species and allowed *Drosophila* to learn multiple dialects. This shows a degree of plasticity in learning abilities which could be adaptive in nature when *Drosophila* species occur in sympatry [83]. This study represents a rare empirical test showing that socially learned behaviors can be transmitted to others (i.e., up to step 3 in Figure 1).

## 5. The adaptive value of social learning

Social learning is an important mechanism in evolution when transmission of socially acquired behaviors is limited to a few generations within a season, such that **traditions** or **culture** will not develop. One can expect that building expertise during a lifetime by social experiences can increase the adaptation rate of populations that are indeed using and memorizing social information, for example for the spatial location of essential resources, even if every adult individual dies at the end of the reproductive season. This is because social information allows individuals to reach, for example, an oviposition site earlier or at lower exploratory costs compared to individuals that explore and spatially navigate without this information. In this regard, most current evidence for social learning, including in non-social insects, concerns behaviors such as foraging and host finding (Table 1), which are based on resources that vary rapidly in space and time notably due

to seasonal changes. Related social information is thus of ephemeral relevance as well and it needs to be updated constantly, suppressing the emergence of any form of longer-term tradition. Rupture of socially transmitted behaviors can also take place because most representatives of insect populations die seasonally, for example during winter in temperate regions. In the latter case, social information about resources can be acquired and exchanged socially *de novo* at the beginning of the new reproductive season each year, starting from newly emerged naïve individuals in spring that learn about resource distribution in their surrounding environment.

Social learning can affect the fitness of individuals, and as such be under positive selection for adaptation to rapidly changing environments. Negative fitness can result from partial or incorrectly interpreted social cues that cause increased energy expenditure in basic tasks such as foraging [82] or mating [102]. The adaptive value of learned behaviors was documented in some vertebrates [4,5]. Experimental evidence of the adaptive value of socially learned behaviors in ecologically relevant conditions currently remains unquantified for the vast majority of remaining living taxa [17,109], including non-social insects [110]. Yet, the costs associated with social learning, including energetic costs and time constraints, and the environmental parameters under which social learning becomes adaptive, have been explored both experimentally [111] and through modelling work [112,113]. These studies have revealed that social learning is not necessarily adaptive under all conditions and that learning can lead to evolutionary traps under rapidly changing environmental conditions [114].

In an intricate study by Danchin et al [100], the authors use the fly *D. melanogaster* to show that traditions and culture can arise and spread throughout subsequent generations. Female *D. melanogaster* made similar mate choice decisions as their teacher when offered a choice between males (colored pink or green) themselves. Transmission of color-based mate preference also occurred when younger females observed older females, meaning that the tradition could spread to a potential future generation. The authors further showed that long-term memory was involved and that mate preferences can be transferred repeatedly over time, leading to a stable mate choice at the level of the population. This study provides a rare example of social inheritance in non-social insects (but see [115] that consider *D. melanogaster* as moderately social). While the potential fitness advantages of mate-copying are clear [99,116], pink and green males do not occur in nature, meaning that there is no ecological relevance and adaptive value of the artificial cue used in this study [117]. Another study on *D. melanogaster* revealed that social learning can increase fitness [84]. Here, the authors exposed ovipositing females to a parasitoid, an insect that lays its eggs inside *D. melanogaster* larvae and subsequently eats and kills it (Figure 1). Being faced with a serious threat to the survival of her offspring [118], females will reduce the number of eggs laid [119]. When a fly subsequently acts as a ‘teacher’ for a naive fly, the ‘student’ will also reduce the amount of eggs laid, even when the original social cue, the wasp, is no longer present [84]. Reducing egg numbers in the face of an immediate threat to offspring survival has a clear adaptive value under natural conditions, because the wasp used in the study actively searches for host patches in the natural environment [120,121], where mating and subsequent oviposition of flies, as well as feeding larvae, generate perceivable olfactory cues [122]. It remains to be tested in this system, however, whether social learning can be transmitted repeatedly from generation to generation (as in [100]).

## 6. Conclusions

**Social learning** and transmission are the stepping stones towards **social inheritance**. We now need to increase our understanding of **social learning** in non-social arthropods and determine its prevalence, both in the laboratory and in the wild. Due to its inherent link to fitness, oviposition site selection offers unparalleled opportunities to study social

learning and transmission, also in systems other than *Drosophila*. The increasing number of studies on **social learning** in non-social arthropods offer promising possibilities for empirical tests of social transmission and **inheritance**.

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## Appendix A

### Glossary:

**Social learning** = Classically defined as “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products” from [3]

**Non-social learning** = Learning based on previous experience that does not involve another animal or its products.

**Social inheritance** = The perception of behaviors performed by others that are subsequently taken over, learned, and spread throughout a population and subsequent generations.

**Culture** = Information or behavior that is acquired from conspecifics through some form of social learning.

**Tradition** = Socially acquired behaviors that are passed from one generation to the next.

**Horizontal transmission of learning** = Learning that occurs from conspecifics within a generation or similar age group.

**Vertical transmission of learning** = Learning that occurs from parents to offspring or from older to younger individuals.

**Oblique transmission of learning** = Learning from unrelated conspecifics.

**Naive individual** = An inexperienced individual.

**Experienced individual** = An individual that has perceived and reacted to a social cue.

**Demonstrator** = An individual that performs a behavior while being perceived by another individual.

**Taught** = An individual that has taken over the behavior of a demonstrator.

**Social cue** = Any information or signal that originates from another individual or its products.

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