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CHAPTER

Culture in Insects

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Abstract

Does culture exist in insects? The answer is probably yes. No insect studies document patterns of behavioural variation among wild populations (i.e. traditions), but some lab studies offer major insight on the mechanisms that can potentially generate traditions. Hence studies on insect culture nicely complement vertebrate studies that often document persistent patterns of behavioural variation among natural populations without necessarily exploring the underlying mechanisms of social learning. This chapter reviews the evidence for insect social learning and suggests that this cognitive capacity is probably widespread in the taxon. The few convincing examples of insect culture, including the proposed case of cultural transmission of sexual preferences in the fruit fly allows testing of an integrative definition of animal culture that is applicable to any kind of animal from insects to vertebrates. The chapter concludes by briefly discussing the challenges for the future of the study of animal culture in insects and beyond.

Keywords: social learning, animal culture, insects, animal culture definition, Vertebate-Insect complementarity

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Introduction

Until the end of the 1980s, the study of culture was mainly human centred. All definitions were designed to capture the specifics of human culture, which made them inappropriate for the study of animal culture. Approaches were also mainly theoretical with relatively few empirical studies. Nonetheless, such human science approaches fostered the emergence of the study of culture in non-human animals in the late 1980s in the framework of behavioural ecology, in relation to the study of animal social learning.

The evidence for animal social learning first came from studies in vertebrates (Galef & Laland, 2005; Heyes, 1994). However, about a decade later, in the 2000s, evidence for sophisticated social learning was published in various kinds of insects, including ants, crickets, fruit flies, wasps, bees, and bumblebees (Coolen et al., 2005; Dawson et al., 2013; Goulson et al., 2013; Grüter & Leadbeater, 2014; Worden & Papaj, 2005; Leadbeater & Chittka, 2007a, 2007b; Leadbeater et al., 2006; Loukola et al., 2020; Sarin & Dukas, 2009; Smolla et al., 2016; Tibbetts et al., 2020). At the same time, the question of the potential existence of animal culture became a new topic in behavioural ecology, which is the domain of evolutionary sciences that studies the evolution of behaviour (Danchin & Wagner, 2008). This favoured the adoption of more experimental approaches in order to study the capacity of social learning to generate collective habits (i.e. local traditions).

The Main Approaches for the Study of Animal Culture

Until the mid-1990s, there were three main approaches to study animal culture (see also Schuppli & Lokuciejewski, this volume). First, as in human studies, theoretical approaches analysed the emergence and potential impact of animal culture (Franz & Nunn, 2009; Lehmann et al., 2008). Second, the study of animal social learning enlightened this field, and raised the question of whether the demonstration of the existence of social learning is sufficient to trigger a cultural process (Brooks, 1998; Danchin & Wagner, 2010; Danchin et al., 2011, 2018). Finally, from the late 1980s, a wealth of data was published documenting the existence of persistent patterns of behavioural variation across wild vertebrate populations (i.e. local traditions), suggesting the existence of animal culture in various mammals and birds (Allen et al., 2013; Aplin et al., 2015; Feher et al., 2009; Kopps et al., 2014; Krutzen et al., 2005; van Schaik et al., 2003; van de Waal et al., 2013; Whitehead, 1998; Whiten, 2007; Whiten et al., 1999; reviews in Avital & Jablonka, 2000; Danchin et al., 2004; Whiten, 2021).

The empirical approach produced only a few experimental studies allowing one to ascertain that the documented behavioural variation across space actually resulted from social learning. Although the existence of local traditions in nature is certainly suggestive of a cultural process, such traditions nonetheless could have a purely genetic or environmental origin in the absence of any social learning. We thus needed to complement these empirical approaches with more mechanistic approaches aiming at demonstrating that the observed traditions do result from evidence that individuals learn local traditions from conspecifics. Here, we have therefore chosen to present the arguments in favour of the existence of cultural processes in insects by outlining evidence that allow us to show empirically that the observed behavioural variation that we call traditions results directly from social learning (see Wild & Hoppitt, this volume, for background regarding social learning).

Insect Social Learning

Today there is ample evidence for the existence of social learning in various insect species. Evidence in insects exists in at least four major biological contexts, including foraging, danger avoidance, choice of egg-laying spot, and mate choice.

Social Learning in Foraging

The first clear evidence for the existence of social learning in an insect was provided by Karl von Frisch with his famous discovery of the ‘waggle dance’ in bees during the 1940s (von Frisch, 1974), a discovery for which he won the Nobel Prize in 1973 alongside Konrad Lorenz and Niko Tinbergen. Frisch showed that after discovering a food source, worker bees (*Apis mellifera*) come back to the hive and perform a special dance called the ‘waggle dance’ that informs other workers of the actual location of the new food source. The waggle dance encodes information about the direction to take relative to the sun position, as well as the energy to spend (i.e. the distance) to fly to get to it. The waggle dance is highly reminiscent of a language in that it is purely symbolic. For example, the angle of the middle part of the dance relative to the vertical on the hive codes for the angle of the direction relative to the sun to take when leaving the hive. Furthermore, if a discoverer stays in the hive for some time, it slowly changes the angle of its dance to continue to indicate the right direction despite the movement of the sun in the sky. In addition, the length of the middle part of the dance indicates the energy to spend to get to the actual source while following the specified azimuth. In the absence of wind, the length of the dance increases by one second for every kilometre.

The waggle dance in itself is surprising, but the most fascinating thing is probably that naïve workers do decode the dance and then go straight to the right place indicated by the worker. By using network-based diffusion analysis Hasenjaeger and colleagues could show that bees recruit others to novel locations via dancing while reactivation to known sites is primarily guided by olfactory cues (Hasenjager et al., 2020). Recently, it was even shown that at least part of the bee waggle dance is learnt socially (Dong et al. 2023, Chittka and Rossi 2023), hence increasing it’s similarity with human language. Today, almost a century after that discovery, the bee dance still constitutes one of the most fascinating examples of social learning in all animals. However, social learning in the context of foraging in insects expands far beyond the sole topic of the waggle dance (Avarguès-Weber et al., 2015). For instance, another example of social learning in the context of foraging was published by Mathilde Baude and collaborators on bumblebees (*Bombus terrestris*) (Baude et al., 2008, 2011). In nature, most insect-pollinated flowers provide nectar to attract pollinators. However, some species, although pollinated by insects, are deceptive in that they do not provide any nectar, and thus constitute real evolutionary enigmas. This is the case for several orchids that often mimic nectar-producing flowers to lure pollinators and get pollinated. Baude used two similar, but distinguishable types of artificial flowers, one providing a sugar solution (provider) and one that did not provide any nectar (deceiver), to create artificial foraging grounds for bumblebees. She found that naïve bumblebees foraging in an experimental field comprising a mixture of deceiver and provider flowers learned far quicker to avoid the deceivers in the presence than in the absence of a trained conspecific forager. However, this effect was only significant when provider and deceiver flowers were patchily distributed, which is often the case in nature. This example corresponds to the social learning strategies ‘copy when uncertain’ or ‘copy when asocial learning is costly’ (see Kendal & Watson, this volume). This kind of approach with artificial flowers has been used regularly to study social learning in a foraging context (e.g. Leadbeater & Chittka, 2005, 2008; Worden & Papaj, 2005; review in Chittka & Leadbeater, 2005).

Still in the context of foraging, which is by far the most studied context for insect social learning, Loukola et al. (2017) revealed unsuspected social learning capacities in bumblebees of an entirely novel task. In this task, bees had to move a ball to a defined location to gain food. They found that naïve ‘bees that observed demonstrations of the technique from a live model demonstrator learned the task more efficiently than did bees observing a “ghost” demonstration (ball moved via a magnet) or without demonstration’ (Loukola et al., 2017, p. 833). This kind of study demonstrates the unsuspected cognitive capacities of insects and suggests that we should never underestimate them (see Brown, this volume, for a similar argument regarding fish).

Several ant species like *Temnothorax albipennis* or *Pachycondyla striata*, who live in relatively small colonies perform tandem runs, where informed individuals guide nest mates to new food sources or nesting sites

(Franklin & Franks, 2012; Franks & Richardson, 2006; Silva et al., 2021). During tandem running, the leader moves backwards after losing contact with the follower in order to keep constant contact with its antennae. They stop frequently so that the follower can learn landmarks or perform path integration. These tandem runs constitute one of the rare documented cases of teaching in animals because they involve costs for the leader as well as bidirectional feedback between the leader and the follower (Franks & Richardson, 2006; see Kline, this volume, for further discussion of teaching).

In insects, the word ‘social’ is often loaded because of the existence of eusociality, and some researchers are reluctant to use that term in the phrase ‘social learning’ in non-eusocial species. However, this is a question of definition. The most widely accepted definition of social learning (i.e. learning from the observation of, or interaction with other individuals or the product of their activity) is independent of the overall level of sociality of the concerned species. Interestingly in this context, the use of flowers of different colours that are rewarding or repulsive allowed Erika Dawson and collaborators to show that even in a eusocial species such as bumblebees, social learning can arise through a simple Pavlovian ability to integrate two learned associations (Dawson et al., 2013). More recently, social learning was also documented between members of different bumblebee species (i.e. interspecific social learning Romero-González et al., 2020), as it was previously suggested in vertebrates (e.g. birds: Forsman, 2000; Forsman et al., 1998, 2002; Mönkkönen & Forsman, 2002; Parejo et al., 2005; Seppänen & Forsman, 2007).

Social Learning about Danger

Insect social learning also exists in the context of danger. For instance, Isabel Coolen showed that naïve wood crickets (*Nemobius sylvestris*) can learn about the potential presence of predatory spiders in the environment by observing the behaviour of conspecifics whom had previously experienced the presence of spiders (Coolen et al., 2005). After spending six hours in a tank with crickets that had spent 48 hours in the presence of spiders, newly introduced naïve crickets hid most of the time and were thus much less detectable to the human experimenter than naïve crickets that had spent six hours with crickets that did not experience the presence of spiders for 48 hours previously. The naïve spiders had clearly learned, probably from observing the behaviour of the experienced demonstrators, that danger was lurking and thus adopted a behaviour that diminished their likelihood of meeting spiders, despite the fact that the naïve crickets never met a spider in the experiment.

Social Learning in Egg-Laying Habitat Selection

Insect social learning has also been documented in the context of the choice of an egg-laying habitat. In this context, Marine Battesti from the group of Frédéric Mery performed a series of cleverly designed experiments. They showed that female fruit flies (*Drosophila melanogaster*) use social information gathered directly from observing experienced demonstrator females (i.e. socially learn) making oviposition site choices, even when they had personal experience with the possible substrates, but stop using social information when they can easily gather additional personal information (Battesti et al., 2012), in an adaptive form of social learning (see Kendal & Watson, this volume). They also showed, in a two-step transmission chain (see Mesoudi, this volume), that the social information that was transmitted from demonstrators to observer flies can then be passed on from observer females to new naïve observer females (Battesti et al., 2012). This suggested a certain level of stability of social information within the group. However, the same team showed that fruit fly females combine their personal preference with social information to choose a laying medium and do not seem to be conformist in this context (see chapter on conformity and Battesti et al., 2015a). The authors later confirmed this hypothesis in an experiment specially designed to study the dynamics of social transmission within a group that regularly receives naïve newcomers (Battesti et al., 2015b). They concluded that 'social learning alone is not enough to support informational stability' (Battesti et al., 2015b, p. 1,) in the context of breeding habitat selection. Note that such stability is one of the major characteristics necessary to foster the emergence of a cultural process. We will come back to this important question in the section on the evidence for insect culture. Still in the context of habitat selection, Loukola et al. (2020) showed that social learning can also exist between individuals of different wild solitary bee species that share ecological requirements.

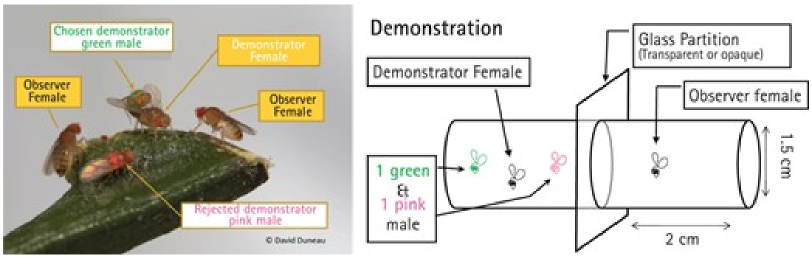
An important conclusion of these results on social learning in breeding habitat choice in insects is that they are highly reminiscent of those described in vertebrates, and particularly birds. For instance, social learning has been clearly demonstrated in habitat choice in several bird species (Boulinier et al., 2008; Doligez et al., 2002, 2003, 2004a, 2004b). Similarly, interspecific social learning in the context of habitat choice in birds recalls the one described in migrating flycatchers (*Ficedula albicollis* and *F. hypoleuca*) that use social information from resident tits (*Parus major* and *Cyanistes caeruleus*, Forsman, 2000; Forsman et al., 1998; Forsman & Thomson, 2008; Seppänen and Forsman, 2007; reviews in Mönkkönen & Forsman, 2002; Seppänen et al., 2007), as well as between rollers (*Coracias garrulus*) and kestrels (*Falco tinnunculus*), using the same nest boxes (Parejo et al., 2005).

Social Learning in Mate Choice

Insect social learning in the context of mate choice is documented in a single non-social insect, the fruit fly *D. melanogaster* (Mery et al., 2009). Social learning in mate choice, which usually is called mate copying (sometimes improperly called mate-choice copying, see Danchin et al., 2020; Wagner & Danchin, 2010), has been demonstrated in many vertebrates, including fish, birds, and mammals including humans (Varela et al., 2018; Witte et al., 2015). Mate copying in the fruit fly (Mery et al., 2009) came as a surprise as it revealed strong mate copying in a non-social insect, which suggested that this species may constitute a particularly interesting animal model to study social learning in a sexual context beyond vertebrates (Leadbeater, 2009). Mery et al. (2009) created two new artificial male phenotypes by dusting them in green or pink powders. Using such males, they showed that after watching a demonstrator female choosing between a green and a pink male for copulation (Figure 1), when later given the choice, an observer female showed a significant preference for the male of the colour she saw being selected during the demonstration. This result was then replicated in different labs, as well as different fly strains, years, experimental designs, and experimenters (Dagaeff et al., 2016; Danchin et al., 2018; Loyau et al., 2012; Monier et al., 2018, 2019; Nöbel et al., 2018a, 2018b, 2022a) with the same conclusion: fruit flies do perform mate copying. That mate copying capacity in the fruit fly later proved to be as effective when using two-dimensional images (or even crudely simplified images) of sexual intercourse instead of live demonstrations (Nöbel et al., 2022b).

Interestingly, two studies failed to detect mate copying in fruit flies (Auld et al., 2009; Belkina et al., 2021). Our experience is that mate copying experiments are particularly delicate, so that they may fail for many purely technical reasons. In carefully reading these two studies, we found many such reasons. For instance, Auld et al. (2009) studying mate copying in *D. serrata* used demonstrations involving females from *D. serrata* (thus providing positive information as copulation occurred) and *D. birchii* with the idea that the latter provide negative information about the concerned male because *D. birchii* females never copulate with *D. serrata* males. This design ignores the well-established fact that all females of any species are under strong selection to be able to recognize conspecifics as copulating with individuals of a different species inevitably leads to drastically diminished and often zero fecundity. Thus, in that experiment, it is very unlikely that *D. serrata* females were fooled by a demonstration consisting of a *D. birchii* female rejecting a *D. serrata* male. This detail could on its own explain the non-detection of mate copying. After all, if there is one thing we learned from studying insect cognition, it is that we should never underestimate their cognitive capacities. For instance, Loyau et al. (2012) showed that *D. melanogaster* females can clearly differentiate two individual males of the same phenotype and with the same copulation history. In short, on top of other details in their protocols, we think that there were many reasons why these two experiments did not provide evidence for mate copying for purely technical reasons.

Figure 1



Fruit fly females watch their copulating conspecifics and adopt their preferences. Left: A typical demonstration-like situation in a natural setting. Here, a 'demonstrator female' choses to copulate with the green male, and not with the pink one, while two 'observer females' watch the copulation. If these observer females later show a significant preference for green males (and vice versa if the demonstrator female had copulated with the pink male) this would demonstrate effective mate copying.

Used with permission from David Duneau. Image created by ED and SN on a picture by David Duneau. Right: The transposition of this setting for mate copying lab experiments. Image created by the authors.

Evidence for Insect Culture

While social learning is inherently necessary for the emergence of culture, demonstrating social learning does not demonstrate animal culture (Brooks, 1998; Danchin & Wagner, 2010). As a matter of fact, social learning is a property of individuals, while culture emerges at the scale of the group and manifests itself through the fact that most, if not all, group members adopt the same behaviour or preference in a given context. We call that common behaviour a tradition. Traditions are highly persistent collective habits that differ among groups or populations. Thus, to demonstrate the existence of animal culture we need to go well beyond the sole demonstration of social learning in order to study how individual social learning can generate a common behavioural pattern at the group scale. More specifically, it is necessary to show that the properties of social learning are such that they can actually lead to a collective and persistent habit (i.e. a cultural tradition), which constitutes the most striking marker of animal culture.

In this context, while there are several compellingly documented examples of insect social learning as we have seen, there are only a few examples suggestive of the above characteristics in insects. Contrary to vertebrates, where much evidence comes from the observation of persistent behavioural variation across populations (i.e. traditions) in the wild, in insects most, if not all, evidence comes from experiments in the lab. One reason is that it is particularly difficult to observe insect behaviour in the wild, while they are particularly suited for lab experiments. The relative scarcity of such examples in insects probably reflects the fact that relatively few studies actually explored the question of culture in insects, as this is not the kind of taxon of which one would *a priori* think to study animal culture. We now discuss the most compelling instances in the next sections.

String-Pulling in Bumblebees

One of the most fascinating examples suggestive of the existence of a cultural process in an insect is that of Sylvain Alem and collaborators. Alem et al. (2016) studied the spread of a new foraging technique within a single colony of bumblebees in lab experiments. Their study design was quite ingenious. They created artificial nectar producing flowers that were visible, but inaccessible because they were below a transparent Plexiglas board. To access the flowers' sucrose solution, bumblebees needed to pull a string attached to the artificial flowers up to the point when the flowers became accessible so that they could suck their nectar-like sucrose solution. Every experimental colony member had an individual tag allowing experimenters to monitor the spread of this new foraging technique among all colony members. The experiment started with the introduction to the colony of a single bumblebee previously trained in accessing the nectar by string pulling. They were able to document the dynamics of transmission of this new foraging technique among colony members. They found that after four days almost all colony members had adopted the new technique while in colonies without a trained demonstrator no colony member had discovered the technique.

These results are surprisingly reminiscent of a cultural process. After all, the new foraging technique rapidly spread among colony members and the adoption of the new technique by a new colony member correlated with its level of interaction with a skilled individual, confirming social learning. Furthermore, after learning the new task some newly skilled individuals became models for other colony members. However, the spread of the new skill was documented only within one colony. Under such conditions, one can question the persistence of that skill beyond the survival of the colony. Indeed, each bumblebee colony survives for one summer and then all colony members die, implying that their knowledge vanishes. This means that a habit that is learned one year will not survive the next winter, implying that there is no information transmitted across generations, preventing emergence of cultural evolution. Indeed, a major characteristic of cultural processes lies in the persistence of the socially learned behaviour *across generations*. This implies that a given behavioural pattern 'A' may change into pattern A_1, A_2, ... A_n, within one generation, but to really evolve (which is an intergenerational process), that history of transmission with change should continue into the next generations. In other words, the concept of culture should incorporate some vertical or oblique transmission. Only under such conditions would we be able to talk of a cultural process and of cultural evolution. However fascinating it is, this is probably not the case in the string-pulling example, as that history will stop unavoidably at the colony death next autumn or winter. Clearly, this reasoning raises the question of how we define animal culture, which is the topic of the next section (see also Schuppli & Lokuciejewski, this volume).

When Can We Talk of Animal Culture?

In the early 1990s several authors working on mate copying claimed that they had demonstrated the existence of animal culture because they had demonstrated the existence of social learning, particularly in the context of mate choice (e.g. Heyes & Galef Jr 1996; and chapters therein, such as the one by Dugatkin, as well as Brooks, 1998; Dugatkin, 1996; Freeberg et al., 1999; White & Galef, 2000). This raised a debate about whether social learning is sufficient to foster the emergence of a cultural process (e.g. Avital & Jablonka, 2000; Brooks, 1998; Danchin & Wagner, 2010). This debate clearly led to the conclusion that social learning was a necessary criterion (Danchin & Wagner 2010; Danchin et al., 2011), but that it was not sufficient. This debate also underlined the necessity to link the study of social learning with approaches reporting the existence of persistent behavioural variation among populations in the wild. It is the existence of such among population behavioural variation, which we call local traditions, that constitutes the best marker of the potential existence of animal culture. Historically, this is how the field of animal culture initiated, by reporting the existence of behavioural traditions (Whiten, 2007; Whiten et al., 1999). But, as we have seen, although that approach is of major interest, it is not sufficient because it is also necessary to show that these traditions are the by-product of some form of social learning. This implies that a full definition of animal culture should have two components: (i) one that concerns the existence of patterns of behavioural variation (i.e. of traditions) and (ii) one that show that such traditions are produced by mechanisms of social learning (see Garland & Rendell, Schuppli & Lokuciejewski, and Whiten, this volume, for further discussion on this issue).

This is what Danchin et al. (2018, p. 1025) proposed in saying that animal culture is the part of ‘phenotypic variation that is inherited through a form of social learning [i.e. learning from others, Criterion 1] …, that occurs across age classes (minimally from older to younger individuals [Criterion 2], is maintained for sufficient time to be copied (Criterion 3), produces trait-based copying [Criterion 4], and incorporates repair or reinforcement mechanisms [e.g. conformity, punishment or information digitization, Criterion 5]’. Lastly, to connect this mechanistic definition with classical definitions focusing on the existence of traditions, it is important to check that the properties of the concerned type of social learning have the potential to generate local traditions spanning over generations.

Cultural Transmission of Mating Preferences in the Fruit Fly

Mate copying is a form of social learning that was particularly suitable for testing the five criteria that define animal culture as we proposed above, as the first criterion of social learning was clearly fulfilled in that system (as we have seen). The challenge was then to test whether that form of social learning actually meets Criteria 2 to 5 in the species. In a series of experiments Danchin et al. (2018) were able to show that all five criteria were fulfilled.

To test Criterion 2 of transmission across age classes, the authors compared the mate copying capacity in two treatments. One in which the demonstrator and observer females were both three days old (as in the experiment reported above), versus one in which demonstrator females were 14 days old, which corresponds to the minimum age of the mothers of the three-day-old observer females in our lab conditions. As they found no statistical difference between these two treatments, they concluded that mate copying is also efficient from old to young individuals, showing that Criterion 2 is met.

Testing Criterion 3 of long-term retention of the socially learnt preference, involved transposing the protocol classically used to study long-term memory involving *de novo* protein synthesis in fruit flies, which demonstrated that when tested 24 hours after demonstration the females showed a clear preference for the males of the colour that was selected by the demonstrator. The test for long-term memory with *de novo* protein synthesis was performed at 24 hours as this is the standard protocol in both humans and animals. In this experiment, females fed with a pharmaceutical drug that blocks *de novo* protein synthesis copied the demonstrators´ preference when tested immediately after the demonstration but were unable to memorize the male colour that mated during the demonstration and were thus unable to copy the demonstrators' choice 24 hours later. Although we did not test memory over a longer term, it has been shown that demonstrating long-term memory with *de novo* protein synthesis most usually leads to very long-term memorization, a capacity that is probably due to the building of a specific structure with those new proteins. Thus, Danchin et al. showed that the building of this long-term memory implies *de novo* protein synthesis, and met Criterion 3.

To test Criterion 4 that the mate copying is not individual based (females learn to prefer male A over male B) but rather is trait based (females learn to prefer males of phenotype A over males of phenotype B, see Bowers et al., 2012 for more details), researchers used several experiments (Danchin et al., 2018; Nöbel et al., 2018b) that together unambiguously showed that females learn to prefer any male of one colour over any male of the other colour, thus fulfilling Criterion 4.

To test Criterion 5 that mate copying is reinforced in some way, we tested whether it is performed in a conformist manner, Danchin et al. (2018) designed a new experimental devicecalled an hexagon allowing them to show several demonstrations simultaneously. In effect, conformity implies that after observing a series of demonstrator females each choosing between a green and a pink male, observer females should later show a (disproportionate) preference for the male of the most commonly chosen phenotype among demonstrations. In the hexagonal device, observer females were placed in a central arena surrounded by six peripheral chambers, each with a female choosing between a green and a pink male. With this device, the authors could manipulate the percentage of males of each colour copulating to create a majority during the demonstrations (from 100 per cent of one colour down to 60 per cent, with a control at 50 per cent). As soon as there was a majority of female demonstrators choosing one colour phenotype, observer females learnt to prefer the most commonly chosen male phenotype with the same efficiency, whatever the level of majority (from 100 per cent down to 60 per cent). As expected, at 50 per cent, observer females chose randomly between male phenotypes.

Finally, using a model of a transmission chain, as well as a real transmission chain in which the learners at one transmission step become the demonstrators of the following transmission step, Danchin et al. (2018) further found that conformity was central to producing local traditions and that under certain model parameter sets, such traditions could persist for over a hundred thousand transmission steps, perhaps representing thousands of generations. Their conclusion was that *D. melanogaster* has all the cognitive capacities to transmit culturally their mate choice preferences in a way that can lead to collective local preferences (i.e. traditions) that can potentially last for thousands of generations. This suggests that we may have to expand the taxonomic range of cultural processes, in order, potentially, to incorporate invertebrates, and more specifically insects.

Conclusions

Studies on insect culture have significantly contributed to the study of animal culture. Such studies have brought about more experimental approaches, as well as a new and tractable definition of animal culture that constitutes a kind of toolbox that can be transposed to any kind of animal species that can be experimentally manipulated to explore the taxonomic range of cultural evolution within the animal kingdom. Importantly, the definition by Danchin et al. (2018) is connected tightly to previous definitions that mainly focused on the existence of behavioural traditions in wild populations. The latter type of definitions remain fully valid when dealing with species such as apes or cetaceans that cannot be manipulated over generations, either for ethical or practical reasons. In such instances, we just need to acknowledge that the claim that the observed persistent-among-population behavioural variation that we call tradition is actually produced by some form of social learning would need further investigation. In most instances that we know of, that interpretation is highly likely to be correct, but this nonetheless remains to be further studied.

Vertebrate and Invertebrate Studies Are Complementary

A major insight brought by insect studies is the fact that in having a relatively short generation time and often having large populations these animals allow us to study the detailed mechanisms of social learning in the exact context of the social transmission (Grüter & Leadbeater, 2014). For example, foraging bumble bees (*B. terrestris*) use social information to complement personal information and do not follow a ‘copy when established behaviour is unproductive’ strategy (Leadbeater & Florent, 2014). Rather, it seems that social learning in bumblebees is a form of associative second-order conditioning (Leadbeater & Dawson, 2017).

In the following decades, we can expect multigenerational experiments in insects to study animal culture. Such experiments would be almost impracticable in most vertebrates (but see Brown, this volume, for similar arguments with fish). In vertebrates, although we know that persistent traditions exist in nature, usually we have only suspicion that these result from social learning because the observed traditions might simply be the result of genetic or environmental variation among groups (although sometimes such alternative explanations can reasonably be ruled out, as in Luncz & Boesch, 2014; Luncz et al., 2012; Thornton et al., 2010). This is the case of chimpanzees in Africa, which constitutes one of the most advanced and fascinating studies on animal culture. After having documented the existence of potential cultural traditions in many aspects of chimpanzee behaviour across tropical Africa (Whiten et al., 1999), the authors studied chimpanzee social learning capacities for one of the concerned behavioural patterns (in a foraging context, Horner et al., 2006). This aided in the interpretation of the observed traditions and whether they were likely to represent a culture, especially in the foraging context (see Whiten, this volume). However, this of course could not cover the full scope of the behavioural patterns that were reported as showing among population variation in the wild. Unfortunately, intergenerational experiments are particularly difficult in vertebrates (a brief review of extant experimental evidence in vertebrates can be found in the introduction of Thornton et al., 2010).

However, insect studies have the mirror drawbacks of vertebrate studies. While the latter are far better at documenting the existence of behavioural variation among natural populations, as far as we know we are lacking this kind of information in insects. For instance, while the fruit fly study reported in the previous section clearly suggests that fruit flies *can* transmit their mating preferences culturally, for the moment we have no clue about whether they actually *do* so in nature. This illustrates the complementarities between vertebrate and invertebrate studies, which thus should work in synergy.

Challenges for the Future

The field of animal culture in insects and any animal in general is facing several challenges. First, it is crucial to amplify the movement from observations alone to a mixture of observation, experiments and modelling to better detect instances of animal culture and to better understand the scope of culture in the animal kingdom. This is the only way to study the mechanisms and the causality between social learning and the emergence of cultural traditions. These approaches should be applied to as many species as possible, without any prejudice. After a decade during which we regularly stated that we did not expect the existence of any cultural process in the fruit fly, we were ourselves stunned by the discovery these animals may be cultural organisms. We must keep an open-minded spirit in this endeavour. In particular, we now need evidence for the existence of insect culture in nature. Another major and highly challenging issue is that we must endeavour to incorporate animal culture into biology as a whole. This is because animal culture constitutes a process of parent–offspring resemblance (i.e. of inheritance), which is usually considered as only resulting from the transmission of the DNA sequence across generations. In other words, the probably widespread span of cultural inheritance makes it necessary to incorporate it into any modern conceptions of evolution. This is probably one of the most difficult challenges facing behavioural ecologists in the future, which is the only domain of evolutionary sciences that can nurture the incorporation of cultural inheritance into the new evolutionary synthesis (a topic that has been at the heart of our group's research for the last twenty years or so; Danchin, 2013, 2023; Danchin et al., 2001, 2004, 2008, 2011, 2019; Danchin & Wagner, 2008, 2010).

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