

An ant's eye view of culture: propagation of new traditions through triggering dormant behavioural patterns

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Abstract We consider a previously unknown way of propagation of behavioural traditions in animal communities using hunting in ants as an example. We experimentally revealed that common litter dwelling ants *Myrmica rubra* effectively hunt jumping prey and the way the hunting behavioural pattern is distributed within ant colonies is rather sophisticated. Comparison of our results with those obtained on vertebrates enables us to suggest that “*distributed social learning*” plays an important role in spreading new traditions in animal communities: initial performances by a few carriers of an “at once and entirely” available behavioural pattern propagate this pattern among specimens which have only dormant “sketches” of it. Spread of these behaviours in populations is based on relatively simple forms of social learning such as social facilitation which underlies species’ predisposition to learn certain sequences of behavioural acts. To be triggered, carriers of dormant “sketches” of a relevant behavioural pattern should encounter performances of this pattern with sufficient frequency. We call this strategy *triggering of dormant behavioural patterns*. Integration of behaviour thus takes place not only at the individual level but at the population level as well.

Keywords Ants · Social learning · Preparedness · Community · Behavioural stereotype · Behavioural traditions · Cultural transmission · Trigger · Stimulus · Hunting · Springtails

Introduction

One of the most fascinating questions of ethology is how genetic and environmental factors interact during the development of behaviour in different species and how novel behaviours spread in populations. The majority of findings on new traditions distributed in animal communities mainly concerns feeding techniques in primates (McGrew 1992, 2004; Boesch 1991; van Schaik et al. 2003). It is still an open question whether a few advanced individuals can propagate stable new traditions within animal communities. There is some evidence that new behaviours, although useful, die with their carriers, and that new feeding techniques may be restricted to only a few individuals from a local population for a long time (Goodall 1986; Gajdon et al. 2006). Which factors limit and which favour the acquisition of new behaviours in animal communities? It might be that preparedness is often the most significant factor even against the background of social learning.

Social learning, as one of the key concepts of cognitive ethology, includes different forms of behavioural displays from relatively simple ones such as “social facilitation” and “stimulus enhancement” to learning by observation (emulation), “teaching” and “cultural transmission” in animal communities (Galef and Laland 2005). Among other forms of social learning, social facilitation deserves a special explanation. *Social facilitation*, in its wide meaning, is defined as an enhancement of performance of the definite

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behaviour when another conspecific is present (Zajonc 1965). Applying the logic of social facilitation to ethology, Clayton (1978) defines social facilitation as an increase in the frequency of a behavioural pattern in the presence of others displaying the same behavioural pattern at the same time. Currently, many authors consider social facilitation a basic form of social learning that can explain by more mundane means some phenomena that have been earlier treated in terms of “animal culture”, such as milk bottle opening by tits and potato washing by Japanese macaque monkeys (for details see Reznikova 2007a).

Although the majority of studies in the field of social learning were made on vertebrates, numerous cases were described in literature where insects appear to learn by observation and thus enjoy complex forms of social learning. As Galef (1996) found, the first hint of observational learning dates back to Darwin’s field notes published by Romanes (1884). Darwin suggested that honeybees learn the habit of nectar robbing by observing bumblebees engaged in this activity. Many excellent experiments in the 20th century demonstrated social bees as being capable of different forms of social learning, from local enhancement, where animals are drawn to sites where conspecifics are present, to “learning from the information centre” where honeybee foragers gain the concrete information from scouts by means of “Dance Language” (for reviews see Chittka and Leadbeater 2005; Farina et al. 2005; Reznikova 2007b). Among non-colonial insects, wood crickets were recently demonstrated as being able to use “public information” to learn about the presence of a natural predator, the wolf spider. In a set of experiments, Coolen and co workers (2005) revealed that the demonstration of fear by experienced crickets provide their naïve companions with an indirect assessment of a local predation threat.

Ants are good candidates for elucidating the role of social learning from the one side and preparedness for certain forms of learning from the other side in implementation of complex behaviours in animal communities. Although the majority of models describe collective decision making in ants as being based on inter-relations of carriers of relatively simple behaviour repertoires (Ratnieks et al. 2006; Couzin 2007), these insects are known as doing many “clever” things including switching between foraging systems (Herbers and Banschbach 1999), information transfer by means of “language behaviour” (Reznikova and Ryabko 1986, 1994; Ryabko and Reznikova 1996) and social learning (Reznikova 2001). It is worth to note that the first experimental proof for observatory learning across species suggested by Darwin for bees was obtained for ants (Reznikova 1982).

Active hunting of ants for jumping springtails has been considered so far only an exotic phenomenon. Although springtails (small Apterygota: Collembola) are abundant

inhabitants of the litter–soil stratum in various natural zones and landscapes throughout the world, they should not be regarded as a readily available prey for predatory invertebrates. Indeed, most species of Collembola have a jumping fork appendage (furcula) attached at the end of the abdomen. The furcula is a jumping apparatus enabling the animal to catapult itself, thereby changing sharply the direction of the springtail’s movement. Of various ant groups, only some tropical species of the tribe Dacetini equipped by snap-on mandibles have been known so far as specialised hunters for springtails (Hölldobler and Wilson 1990). We were first to reveal that *Myrmica rubra* can effectively switch to jumping springtails (Collembola) as a mass prey (Reznikova and Panteleeva 2001, 2005). The finding of a new form of the complex hunting behaviour in *M. rubra* enables us to examine how this behavioural pattern spreads in local populations. Three hypotheses have been examined: (1) “a prey as a releaser”: the majority of ants have the genetic template of a potential prey, and prey stimuli are sufficient for an ant to develop the hunting behaviour independently; (2) “cultural transmission”: first specimens catch springtails by chance and then improve their art; others learn to hunt jumping prey by observation; social learning strongly dominates over inherited preparedness for special hunting behaviour; (3) “dormant incomplete behavioural patterns”: ants possess innate behavioural program of different completeness. Those specimens that are equipped with the complete pattern enjoy both innate template of a potential prey and a readily available hunting stereotype; others possess dormant fragments of the pattern and complete them by means of simple forms of social learning.

Materials and methods

Experiments were carried out at the forest park zone near Novosibirsk and in the laboratory. Field experiments were aimed at examining ants’ ability to catch springtails effectively and switch to them as a mass prey. We chose six *M. rubra* colonies in sites with different levels of population density of Collembola. The dynamic density of Collembola was estimated with the use of a transparent plate (225 cm²) placed on the surface of litter. Springtails were counted at four plots (ten sessions each) near each of the six ant nests. In order to estimate the fraction of springtails in ants’ food under natural conditions, the food units brought by *M. rubra* to the nests were counted for 2 days at each colony. Ants’ activity was monitored during periods from 9.00 to 12.00 A.M. and from 17.00 to 19.00 P.M. (a total of 60 h). Then, fractions of Collembola in food spectra of colonies were compared at sites with different sizes of springtail populations. Three nests were in the areas

Table 1 Comparative data on ants–springtails relations in *Myrmica* colonies living in places with different population densities of Collembola

No. of <i>M. rubra</i> colonies	Springtail population density: number of specimens per 225 cm ² (mean value averaged 40 records ± SE)	Number of attacks of ants toward springtails in containers per minute (mean value averaged over 20 ants ± SE)	The fraction of springtails in the natural food spectrum (%)
1	0	0.35±0.6	0
2	0	0.20±0.3	0
3	2.10±0.4	0.54±0.09	17
4	6.8±1.56	3.10±0.53	36
5	6.8±1.56	3.31±0.57	80
6	8.1±1.25	7.30±1.33	100

of rich abundance of springtails whereas three others were in the areas of limited availability of this prey (see Table 1).

In order to observe the process of hunting in field experiments, we placed live springtails *Tomocerus sibiricus* into glass containers (diameter, 6 cm; height, 12 cm) with gypsum bottom, 30 specimens per container (Fig. 1). We maintained a constant number of live springtails within containers by adding individuals as required. The density of springtails in containers imitated natural conditions in sites with large size of springtail populations. A transparent substrate (chopped plastic bottles) was added to container to simulate forest litter and make video recording easy. The containers were dug in soil near the same six ant nests which were used to measure the natural hunting activity, one container per nest, at the distance of 30 cm from the entrance. The experiments were carried out outside the periods of monitoring food units. The number of aggressive contacts of ants with springtails was counted in habitats with high and low abundance of Collembola. To do this, we took 20 ants from the feeding area of each ant colony and



Fig. 1 A glass container with gypsum bottom and transparent substrate dug in soil near an ants' nest. Photo by S. Panteleeva

placed them one by one to the experimental container with the use of a small brush. Ants' behaviour was monitored individually, from the moment of placing a specimen into the container until it left the container. We evaluated mean values of numbers of attacks per minute averaged over 20 ants. After each trial, containers were removed from ants' feeding territory so that ants had no possibility to visit them between trials. The total time of observation in containers was 160 h.

In the developmental study in the laboratory, we compared the hunting behaviour towards jumping springtails *T. sibiricus* of the one "wild" (control) *M. rubra* colony (500 completely matured workers of unknown age housed with a queen) and four naïve colonies (300 workers with a queen in each colony) raised from pupae in separate laboratory nests and deprived of the experience of communication with adult ants (except for queens but the queens in *Myrmica* do not demonstrate any elements of hunting behaviour) as well as with potential prey. The control colony as well as pupae for raising naïve groups were taken from sites with high density of springtails. All pupae were at their late stage, and they did not need help of adult nest mates to emerge. When young imagos emerged, we added packets of eggs and small larvae in order to motivate young ants to hunt. As a result, both "wild" and naïve colonies contained brood in numbers sufficient to force hunting activity in ants. As it is known, ants hunt for protein food in order to provide larvae with nutrient. In the absence of prey, they feed larvae with special nutrient eggs laid both by the queen and workers (Brian 1973).

We isolated naïve ants from contacts with adults in order to deprive them of any outgoing signals concerning specific behaviours. This allows us to judge which behaviours awake developmentally, and which need signals from experienced workers. It was demonstrated earlier that fully naïve ants accomplish such a complex behavioural pattern as aphid milking being lack any signals from adults (Reznikova and Novgorodova 1998; Reznikova 2007a). So, in principle, we could expect naïve ants to hunt springtails as well just after encountering and discerning potential prey.

To observe the interaction of the ants with active prey, we put them one by one into containers with 30 live springtails. Ants' behaviour was monitored individually, 15 min per ant. After each session the containers were removed from the arena, so that ants could not access them during non-monitored periods. In naïve colonies, 123 individually labelled ants were tested 2, 7, 14, 30 and 60 days after the pupae turned into imagoes. According to Brian's (1973) study, behaviour in *Myrmica* ants is fully matured at the age of 30 days, and our experiments on *M. rubra* confirmed this (Reznikova and Panteleeva 2005). In sum, we carried out 209 sessions with 123 naïve ants and 214 sessions with 127 members of the control colony (see Tables 2 and 3). The total observation time in these series of experiments was 80 h. In order to obtain more specific data on the relationships between naïve ants and their potential prey, we conducted a special series of experiments in which six naïve ants were placed separately into containers with Collembolans for 20 h each; in another series, we placed 25 naïve fully matured ants (of age between 1 and 2 months) and 25 wild individuals into containers with springtails one by one and allowed them to stay there for unlimited time. In both series of experiments, all contacts between ants and springtails were observed.

It is worth to note that in all colonies specimens were genetically variable because each mother colony contained no less than 20 queens. Although we examined the ants from one control colony only, we thus tested many genetically different individuals, and the same was with four naïve groups.

Results

From previous studies, we know that the success of ants' hunting correlates with the abundance of springtails in their habitat. Earlier (Reznikova and Panteleeva 2001), we

Table 2 Reactions of members of the control *Myrmica rubra* colony to springtails in the laboratory containers

Number of ants tested from one to six times	Number of ants displaying the following reactions:			In total
	Each time caught a prey	Attacked but failed to catch	Caught a prey at least once	
One time tested	35	41		76
Two times tested	10	8	16	36
Three times tested	2	0	5	7
Four times tested	1	1	3	6
Five times tested	0	0	1	1
Six times tested	0	0	4	1
In total	48	50	29	127

Table 3 Numbers of naïve *Myrmica rubra* tested at different ages in the laboratory containers with springtails

Ants' age	2 days old	3–7 days	8–14 days	20–30 days	60 days
Number of ants tested	10 28	10 23 18	10 21 12 13	10 9 8	9 9 8 11 0
In total	38	51	56	27	37

Numbers in each line reflect how many ants were tested and at which age. For example, from ten ants tested at the age of 2 days, all were tested at 3–7 days, 8–14 days and 20–30 days, and nine of them were tested when they were 60 days old. From other 28 ants tested at 2 days, nine were later tested at the age of 60 days, and none of them were tested at the intermediate ages. Twenty-three individuals were tested at the age of 3–7 days, and 21 of them were subsequently at the age of 8–14 days

investigated 11 colonies of *M. rubra* by means of field experiments in which ants could freely visit containers with springtails placed in them. In three colonies living in sites rich of springtails, we observed 71 ants' visits into containers and in 47 of them springtails were successfully caught. Other visits were marked by ants' vigorous attacks toward potential prey but they failed to catch it. It is important to note that members of *Myrmica* colonies living in sites poor of Collembolans did not catch live springtails in the containers. We observed two cases where springtails died in the containers, and ants immediately picked them up. However members of these colonies took a weak interest in moving prey. From 40 ants that visited the containers, 11 performed single attack attempts towards springtails but none ended with ants killing springtails.

In current field experiments, we concentrated on measuring numbers of attacks towards springtails in ants forcibly placed into containers one by one. It can be seen from Table 1 that ants from three colonies living in sites with large size of springtail populations made ten times more attacks towards springtails than members of other colonies. This correlates with the fraction of springtails in ants' prey revealed in the control of food units. It is seen from Table 1 that numbers of ants' attacks toward springtails highly correlates with the fraction of springtails in colony's food spectra. It is natural that the higher population density of Collembolans in the site the more springtails are detected in ants' food spectrum (the value of Spearman's rank correlation coefficient is 0.94 at $p < 0.05$).

Our observations on how ants behaved in containers showed that members of the colonies studied distinctly differed from one another in relationships with the potential prey. Members of the colonies living in sites rich of

springtails demonstrated searching for the prey and sufficiently specific hunting behaviour. These ants moved relatively fast and freely through the bulk artificial litter. Once the ant found itself in the immediate proximity to a springtail, it attacked the prey, and in the case of a successful catching attempt, the prey was immediately transported to the nest. Hunters behaved purposively, and they made, in average, from three to seven energetic attacks towards the prey per minute (Table 1). Some particularly purposeful hunters were able to kill and transport to the nest up to seven springtails one after another. Members of the colonies living in sites poor of springtails behaved rather indifferent towards potential prey. Being forcibly placed into the container, the ants either buzzed on a wall or left the container after 1–2 min not displaying any reactions on the moving prey.

Could it be a case of “cultural transmission” of gained experience in ants, that is, could it be that members of colonies frequently clashing with springtails learn hunting by observing successful hunters? The next step was to reveal the role of a specific prey as a releaser in springtail hunting and the role of social learning, that is, to test and compare the first two hypotheses (“a prey as a releaser” and “cultural transmission”).

It was revealed in laboratory experiments that members of the control (“wild”) ant colony taken from a place with high density of Collembolans caught jumping springtails rather effectively: 116 of 214 tests ended with catching the prey; in the remaining tests, ants also responded to the springtails aggressively (Fig. 2). We tested 127 individuals, from one to six times each of them (Table 2). From all ants examined, 77 specimens (the sum of the first and the third columns in Table 2) caught at least one springtail during the limited period of 15 min. One can see from Table 2 that from 36 ants tested two times, ten caught a springtail twice and 16 once; one individual was lucky to seize a prey four



Fig. 2 An ant seizing a springtail. Photo by S. Panteleeva

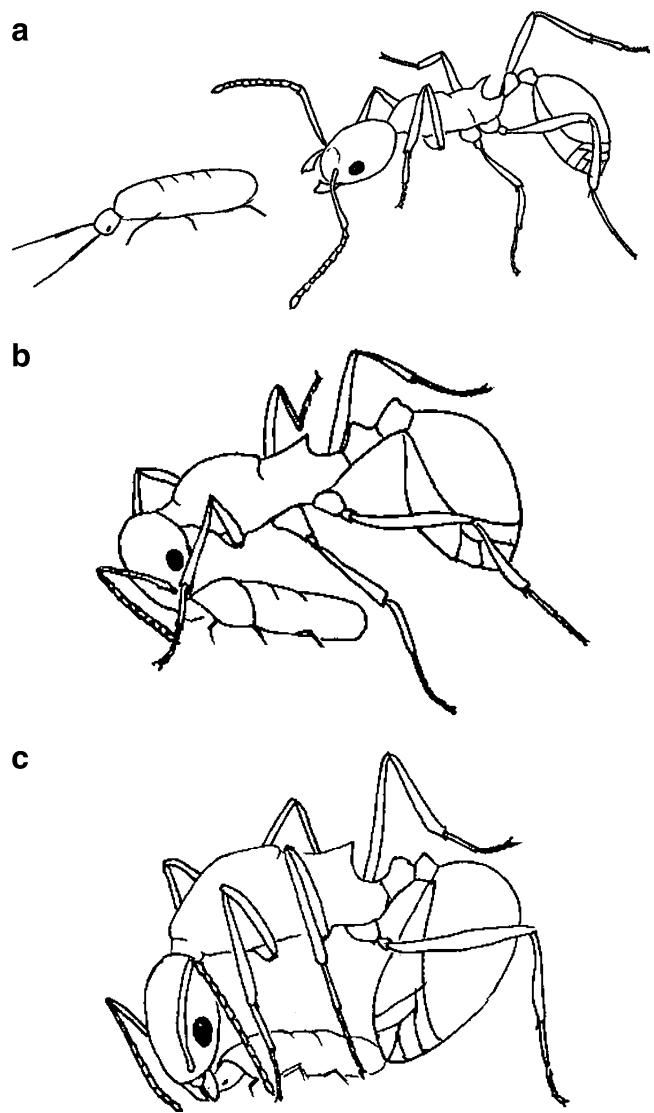


Fig. 3 a, b, c The sequence of actions of a *Myrmica* ant when it hunts a jumping springtail. Drawings by S. Panteleeva

times one after another, and two ants did so three times. From 127 ants, 50 failed to seize a prey during a 15-min period but all of them made energetic attacks; there were no ants indifferent towards potential prey.

All successful springtail hunters demonstrated behaviour which was sufficiently specific. Once the ant found itself in the immediate proximity of a springtail (Fig. 3a), it attacked the prey, bent the abdomen and head to the thorax, jumped to the springtail (Fig. 3b), fell on it abruptly and stung (Fig. 3c). We call this stereotype “tip-and-run attack”. Hunting ants demonstrate this stereotype frequently: indeed, all attacks ended with ants killing springtails were “tip-and-run attack”, and energetic aggressive attacks that ended with ants missing the prey can be called “unaccomplished attacks”. We do not consider this stereotype specific for catching springtails; it is possible that ants can apply this stereotype to

catch other types of prey possessing definite shape, size and style of movement. Further experiments are needed to examine whether *Myrmica* can generalise “tip-and-run attack” to catch other types of difficult-to-handle prey.

In contrast to “wild” ants, laboratory-raised naïve ants behaved rather peacefully towards potential prey. Naïve ants treated springtails in the same friendly manner as if they were nest mates, and they frequently got in touch with them antennae to antennae (Fig. 4). However, from 204 tests, seven ended with naïve individuals killing the springtails. We will consider these cases below in detail. As it was noted before, in the control colony, 116 of 214 tests ended with springtails being caught. Obviously, this difference is significant: the value of χ^2 is 120 (that many times exceeds 3.841 sufficient for 0.01 value of significance).

In a special experiment, 25 naïve ants and 25 “wild” (control) ants were placed into the container with springtails one by one, and they were allowed to stay there for unlimited time. There was no significant difference in the duration of time that members of the naïve colony and of the control one spent in containers. From naïve ants, six individuals spent less than a minute in the container, five spent 12–76 min there and others abode with potential prey 1–5 min. From “wild” ants, seven individuals spent less than a minute in the container, ten spent 10–42 min there and eight stood in the container for 1–8 min. But, as expected, reactions on the potential prey differed essentially between the naïve and the “wild” ants. All contacts observed between the naïve ants and springtails were peaceful, and multiple antennal contacts between them were observed. From 25 ants tested, five individuals did not touch Collembolans (although two of them abode between 3 and 4 min with the potential prey), 16 ants contacted with springtails from one to seven times and four individuals quietly touched the potential prey from nine to 14 times.



Fig. 4 A naïve ant treats springtails in a peaceful manner, as a nest mate. Photo by S. Panteleeva

Members of the control colony exhibited both aggressive contacts (unaccomplished attacks and tip-and-run attacks) with the prey and non-aggressive ones. The latter apparently differed from peaceful treatment of the potential prey by naïve ants: members of the control colony gave only fleeting touches to springtails, for the time being indifferent. However, we can consider all “non-aggressive” contacts together. Then, from this experiment, we have 164 aggressive (155 unaccomplished attacks and nine tip-and-run attacks) and 32 non-aggressive contacts with springtails in members of the control colony, and in naïve ants these values are 0 and 104 correspondingly. Obviously, this difference is highly significant.

In another experiment, six naïve ants were forcibly placed into separate containers with springtails for 20 h. Despite hundreds of contacts with potential prey, none of them demonstrated attacks.

All these observations show that stimuli coming from springtails do not awake hunting behaviour in ants and enable us to reject the first hypothesis (“a prey as a releaser”).

Now let us consider those seven of 123 naïve ants that caught springtails in the first experiment. Surprisingly, they were able to catch and kill the prey spontaneously and successively, and all of them exhibited the “at once and entirely” available hunting behavioural pattern which had no noticeable differences from that of the control ants. One of these individuals caught the prey twice at the very early age of 7 days, and the others did this once at the age of 14 days (also relatively early). In contrast to the control ants, they abode with their prey on the laboratory arena instead of transporting it to the nest and feed larvae there. Thus, the hunting in the naïve colonies “ran idle”, i.e., the prey was not used for its intended purpose. This means that a few naïve ants possess inherited hunting stereotype sufficient to catch a difficult-to-handle prey but their hunting behaviour should be improved in the course of the ontogenesis of imagos. Apparently, such “born hunters” should encounter potential prey rather frequently to improve their art of hunting. It is possible that being uncalled for the hunting stereotype falls asleep.

Indeed, this is a striking observation demonstrating the difference between the majority of specimens that do not react to the live prey and a few individuals that spontaneously and readily catch and kill the moving prey and thus may be called “born hunters”. These results enable us to prefer the third hypothesis (“dormant incomplete behavioural patterns”) over the second one (“cultural transmission”).

Discussion

The complex specific stereotype of hunting behaviour in ants that we call “tip-and-run attack” may be expressed as

an integrated set of behavioural sequences applied for catching active jumping prey such as springtails. Even if we had found only one ant that exhibits the “at once and entirely” available hunting behavioural pattern, this would be sufficient to suggest the presence of genetically programmed sequence of behavioural acts. The fact that several completely naïve ants turned out to be carriers of the whole complex hunting stereotype while the rest remained rather indifferent to the potential prey enables us to consider the leading role of preparedness in the development of this behaviour. Thus, based on the experiments conducted, we suggest that the main form of expansion of this specific hunting stereotype within an ants’ colony is “*distributed social learning*”: initial performances by a few carriers of an “at once and entirely” available behavioural pattern propagate this pattern among specimens which have only dormant incomplete “sketches” of it. The hunting stereotype may be present in a cryptic form until an ants’ colony faces mass reproduction of new prey in their local place. Spread of hunting behaviours, new for an ants’ local population, could be based on relatively simple forms of social learning such as social facilitation. The presence of individuals equipped with an inherited complete stereotype is necessary for triggering this stereotype in other members of the population. Members of ant colonies that are equipped with “at once and entirely” available hunting stereotype dwelling in places with large size of springtail populations have good possibilities to exhibit tip-and-run attack, and other members of the colonies encounter these attacks with sufficient frequency to trigger their dormant fragments of behavioural patterns and combine them into complete sequences of behavioural acts.

We have arrived at this conclusion by excluding two alternative possible explanations: (1) that the majority of ants have a genetic template of a potential prey, and stimuli gained from prey are sufficiently complete to develop the hunting behaviour independently (“a prey as a releaser”) and (2) that first specimens catch springtails by chance whereas others learn to hunt jumping prey by observation, that is, social learning is strongly dominated over inherited behaviour (the hypothesis of “cultural transmission”). Note that this hypothesis presupposes rather complex forms of social learning such as emulation, that is, animals’ ability to learn by observation how environment works (Tomasello et al. 1987). In principle, it was experimentally proved that ants are able to learn to solve rather complex problems (such as finding food in a maze) by observing how other ants do this (Reznikova 1982, 2001). However, in the case of propagation of complex hunting behaviour in ants’ colonies, it seems more parsimonious to prefer the third hypothesis that the presence of individuals equipped with an inherited complete stereotype is necessary for triggering

and completing this stereotype (yet incomplete) in other members of the population. We call this strategy *triggering of dormant incomplete behavioural patterns*. Further experiments that would help to confirm our conclusion, such as extracting the few carriers of the whole ready stereotype and moving them to the group of non-hunting ants, are scheduled for the future. Besides, special observations are needed to clarify the role of immediate contacts between “born hunters” and naïve foragers in the shaping of springtails hunting. However, we consider the obtained results sufficient to support our hypothesis. At this stage of our knowledge, we suggest that carriers of whole patterns to be spread serve as catalysts of social learning by relatively simple means of social facilitation. Triggering of dormant incomplete behavioural patterns can be based on a cumulative effect and then tuned by individual experience of observers.

Development study of tool use in New Caledonian crows is perhaps supportive for our hypothesis. These birds are known as the most prolific avian tool users. Explorers of tool using in this species have elaborated a hypothesis about cumulative cultural evolution (Hunt and Gray 2003). However, recent experiments with four hand-raised juvenile individuals showed that one chick spontaneously manufactured and used tools in a sophisticated manner, without any contact with adults of its species (Kenward et al. 2005). It is possible that this luckily found chick belongs to the same club of carriers of “at once and entirely” available behavioural patterns as our several young springtail hunters.

Comparison of our results on hunting *Myrmica* with those obtained on vertebrates enables us to suggest that it could be adaptive for members of different species to have dormant “sketches” of complex behavioural patterns being implemented on several carriers and then distributed by means of social learning. This type of social learning can be called “distributed social learning” because fragments of useful behavioural programs are distributed among members of a population and remain cryptic until appropriate changes in the environment occur, such as climate changes or appearance of new abundant prey, or new predators and so on. Indeed, it could be rather costly for animal brains to be equipped with complex stereotypes for all possible vital situations. Propagation of complex stereotypes, new for certain populations, is based on relatively simple forms of social learning such as social facilitation which underlies species’ predisposition to learn certain behaviours and does not require feats of intelligence from animals. In the absence of such predisposition in “pupils”, new behaviours would die with the death of “tutors”. The alternative for the animals is to be intelligent enough to quickly grasp and spread innovations. It might be that this option is implemented in some populations of primates (Whiten et

al. 1999) and dolphins (Krützen et al. 2005) but it also might be that even in cases of “real teaching” we meet a combination of innovative and preconditioned behaviour.

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