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The wisdom by social learning

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V přírodě existují tyto tři zdroje učení: genetická dědičnost, individuální učení a sociální učení. Sociální učení probíhá tak, že se učíme buď od ostatních, s ostatními nebo o ostatních. Jedinci, kteří se učí pomocí ostatních, sledují je, mohou vykazovat následující formy sociálního učení: mohou vykazovat zvýšený zájem objevovat, potom co jsou zaujati sledováním činnosti nějakého modelu (sociální napomáhání); mohou být přitahováni k objektu, s kterým model manipuloval (zvýšená stimulace); mohou se účastnit stejného, pro druh typického chování (jako „nakažení"); mohou se naučit něco o vztahu mezi daným stimulem a posílením odměnou při správné reakci (podmiňování pozorováním); mohou se naučit něco o vlastnostech nebo možném využití podnětu (učení napodobováním); mohou se naučit demonstrovanou činnost (napodobování).

Introduction

Members of many species spend a great part of their time in the company of conspecifics. Animals can assimilate essential information by observing their companions, that is, when, where and what to eat, with whom to mate, whom to fear, and how to spend spare time if there is some. In principle, all information can be picked up from internal resources, by development of inherited program. However, social learning and communication give animals great possibilities to improve adaptability and flexibility of behaviour in conformity with concrete and changeable vital circumstances. In many natural situations boundaries between flexibility and conservatism are rather fuzzy. Social learning can sometimes generate behavioural traditions, and some of these traditions can be paradoxically conservative and thus hardly distinguishable from innate forms of behaviour by displays. If we want to know what part of a whole repertoire falls to the share of social learning, we definitely can not gain this knowledge in the mind‘s eye; instead, we should conduct developmental studies and carry out special experiments. In modern ethology and comparative psychology studying of social learning is a specific and rapidly developing direction with its own notions, definitions and hypotheses. We will consider different forms of social learning, from relatively simple such as social facilitation, to the most complex such as tutoring and maintaining traditions in animal societies. In general, we will develop a concept of how animals acquire information and skills from other individuals by means of observations on their behaviour.

Different forms of social learning

Social learning is said to occur when the behaviour, or presence, or the products of the behaviour, of one individual influence the learning of another (Caldwell and Whiten, 2002).

One of the most complex manifestations of social learning is *imitation*. Thorndike (1898) defined imitation as “learning to do an act by seeing it done”. Basing on his studies of insightful behaviour of animals, Köhler (1925) suggested that imitation demands elements of consciousness and understanding of that a modelling subject possess similar features with the learner. Imitation occurs when observers learn about responses, actions, or patterns of behaviour as a direct result of conspecific observation (Heyes, 1993). Call and Tomasello (1996) insist that for “true” imitation to occur the observer needs both to recognise the goal of the demonstrator and to realise that reaching this goal is only possible by copying the acts of the demonstrator.

The power of simpler than “true imitation” forms of social learning has been underestimated for a long time. “Social learning” in its recent meaning includes a wide range of categories of different levels of complexity. Several phenomena that were once seen as clearly imitative have since been explained in terms of simpler mechanisms resembling imitation.

Contagious behaviour is exemplified by a rule such as “if others are fleeing, flee also”. The idea is that the stimuli produced by the performance of a particular behaviour serve as triggers for others to behave in the same way. Possible examples of contagious behaviour include flight responses, movements in flocks or shoals, and chorusing by birds, frogs, and dogs. Laughing and yawning are good examples of contagious behaviour in humans. Zentall (1996) argues that contagious behaviour must have a genetic basis, i.e. it must involve the triggering on of the instinctive response.

Social facilitation, in its wide meaning is defined as an enhancement of performance of definite behaviour when another person is present. Originally, the theory of social facilitation was intended by Zajonc (1965) to explain the effects of an audience on human performances. The presence or action of the demonstrator might affect the motivation state of the observer that eventually leads to better performance. Recently 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. We will further consider these examples in details.

Stimulus enhancement (Spence, 1956; Galef 1988) is said to have occurred when the presence of an individual draws an observer’s attention to a particular object, thus enhancing the observer’s opportunity to learn about the object. The result of this narrowing of behavioural focus is that the individual’s subsequent behaviour becomes concentrated upon these key variables. The observer does not copy actions of the demonstrator, and the actual actions of the observer are acquired on the basis of trial and error.

Social facilitation and stimulus enhancement from more experienced individuals can serve as proximal mechanisms fostering safe incorporation of novel foods, spread of knowledge about predators and other dangers, and even increasing effectiveness of mate choice.

Observational conditioning takes place when the demonstrator’s actions provide the observer with the opportunities to learn that the appearance or movement of an object signals the occurrence of an appetitive or aversive event. The observer thus learns the relation between some part of the environment and the reinforcer, that is, a Pavlovian association may be established (Zentall and Levine, 1972). Socially-transmitted food preferences (Galef, 1988) represent a special case of observational conditioning. The mechanisms responsible for socially-acquired food preferences appear to have strong simple associative learning components (e.g., learned safety or the habituation of neophobia to the novel taste), for which the presence of a conspecific may serve as a catalyst. Furthermore, these specialised mechanisms may be unique to foraging and feeding systems.

One of the best examples of observational conditioning is in the acquisition of fear of snakes by laboratory-reared monkeys exposed to a wild-born conspecific in the presence of a snake. In their experiments Mineka and Cook (1988) showed that lab-reared rhesus monkeys can acquire a fear of snakes by observing other monkeys expressing fear of snakes. When non-fearful lab-reared monkeys were given the opportunity to observe a wild reared demonstrator displaying fear of live and toy snakes, they were rapidly conditioned to fear snakes. The fear response was learned even also in those cases when the fear-demonstrating monkey was shown on a videotape. Then the most intriguing stage of experiments followed. Videos were edited so that identical displays of fear in the demonstrating monkey were modeled in response to toy snakes and flowers, or to toy crocodiles and toy rabbits. The lab-reared monkeys showed substantial conditioning to toy snakes and crocodiles, but not to flowers and toy rabbits. These results provide a strong support for selective (guided) learning which is probably based on a specialized behavioural module. This study also illustrates how observational conditioning occurs. Presumably, a fearful conspecific serves as the unconditioned stimulus, and the snake serves as the conditioned stimulus. It appears that exposure to a fearful conspecific or to a snake alone is insufficient to produce fear of snakes in the observer.

When observation of a demonstrator allows an animal to learn how the environment works, a form of learning is involved which has been labelled "emulation" (Tomasello et al., 1987). Whereas stimulus enhancement changes the salience of certain stimuli in the environment, emulation changes the salience of certain goals (Byrne, 2002). In "emulation" the learner gains information from observing a demonstration, but in achieving the same goal, may use a different method. The investigation which prompted the recognition of this process involved chimpanzees learning from a trained conspecific how to rake food items into a cage (Tomasello et al., 1987). The data showed that chimps exposed to the skilled demonstrator learned how to use the rake, unlike controls, who were unsuccessful in the task, despite manipulating the tool just as often. Animals, however, did not copy the precise strategy employed by the trained conspecifics. Instead, the observers were learning from the demonstration the "affordances" of the tool. The meaning of "emulation learning" (Call and Tomasello, 1994) has expanded to incorporate observational learning about the properties of objects and potential relationships among them. Emulation can also account for findings of observation learning that have been earlier treated as imitation.

Ecological aspects of social learning

Opportunity for the exchange of information among individuals is one of important benefits of living in groups. Species differ in their abilities to use socially acquired information and, in particular, in their abilities to learn through traditions. Members of social groups often monitor the behaviour of their companions in an attempt to gain information about the location of foraging sites or approaching predators. In many cases, for group living animals the only socially acquired information available to individuals is the behavioural actions of others that expose their decisions, rather than initial stimuli on which these decisions are based. So an individual has to make a choice between possibilities to use socially generated cues or to rely on a personal decision basing on the stimuli that gained directly from its environment. A readiness to pay attention only to socially generated cues can reflect a level of conformity of an individual or of a whole group.

A role of social learning in foraging. The idea that animals may observe others to get information about resource quality arose mostly in foraging context (for a review see: Danchin et al., 2004). Animals can use socially gained cues in the context of searching patchy distributed food or making decision about food availability and appropriateness.

Social facilitation of eating novel food has been found in many species. Animals living in groups monitor each other every moment of their periods of activity and react on specific motions which send messages that food is available. For example, Brown and Laland (2002) have shown that the specific darting motion serves a cue to naive fish to learn to forage on novel prey items. They found that 100% of the individuals that paired with pre-trained fishes learned to accept the novel prey. Naive fishes paired with equally naive individuals actually performed worse (50%) than the individuals learning in isolation (73%).

It is easier for many species to acquire food preference socially than to learn by themselves to avoid food that is poisonous. In Galef et al.'s (1985) elegant experiments with rats some of the critical features of the social interactions preceding formation of food preference have been revealed. The experimenters used a simple apparatus to allow one rat to smell food on an anaesthetised demonstrator rat. An observer rat was placed into the basket of the apparatus, and an anaesthetised (and thus unintentional) demonstrator was placed into a wire mesh basket. Some demonstrators had food dusted on their faces, and others had food placed directly into their stomachs through a tube. In both cases the observers subsequently showed a preference for the flavoured diet that had just been fed to the demonstrator. However, if the rear end of the demonstrator was dusted with food and placed foremost in the basket, then only a slight preference for the food was demonstrated. Finally, if a wad of cotton wool, rather than a rat, was placed in the basket, then despite being dusted with food, there was no change in the attractiveness of the food. Thus the demonstrator does not need to be active to encourage the development of a food preference in another rat. But the demonstrator should be a rat, and the observer must be sure that the demonstrator touched the food by its face, not by a tail!

In experiments with domestic hens Sherwin et al. (2002) have demonstrated that avian social learning should be not fundamentally different that of mammals, and the similar features of the social interactions influence food preference in these groups of animals. In particular, it turned out that the more enthusiastically a demonstrator pecks novel food items, the more items observers consume.

Mate choice copying. It is an intriguing question to what extent social factors can influence the choice of sexual partner. Female mating decisions are often influenced by exposure to the mating interaction of others. This style of mating behaviour is called “mate choice copying” which is said to occur when the probability of an individual selecting another as a sexual partner increases because other individuals (of the same sex) have selected the same partner. Mate choice copying has been reported in several species of birds and fishes. To estimate the role of social information in mate choice, it is necessary to separate the signals deliberately produced by displaying males from the cues that are inadvertently produced by females that make their choices.

Dugatkin (1992) has elaborated an experimental paradigm to investigate this problem. In his study on guppies two males were secured at the ends of an aquarium, one with a demonstrator female nearby. The observer, another female, placed centrally, watched the other female interact with one of the males. When, after the demonstrator has been removed, the observer was allowed to choose between the two males, she consistently chose the male that the first female chose. Multiple comparisons with choices that were made by control females enabled researchers to suggest that females follow a rule: “if this male is good for another female, he is good for me”, that is, they utilise the presence of the female near a male as an indication of his quality (for a review see: Brown and Laland, 2003).

Galef and White (2000) have suggested an interesting experimental technique in order to explore social influences on reproductive behaviour. They used Japanese quail (*Coturnix japonica*) as a model species. Researchers changed typical look of birds by adding them a novel trait, namely, a white hat. Females that observed that males with novel traits mated successfully preferred males that possess similar white hats.

These studies show that mate preference can spread rapidly through population by social mechanisms, affecting the strength of sexual selection.

Public information about danger. Acquiring information about danger such as predators by use of social cues can sufficiently decrease the level of lethal risk for group living animals. Utilising information gained from observing conspecifics is especially advantageous as it allows adopting appropriate behaviours without the need to independently verify the approach of a predator.

The general tendency to copy flee-responses of an entire group (flock, herd, or shoal) is based on a simplest form of social learning, namely, on contagion. A panic reaction of a single individual can trigger similar reactions of other members of the group. Individuals react to the flight response of neighbours rather than directly to the advancing predator itself. Synchronous predator responses seem to be cooperative at least in some species. For example, in herrings’ schools, attacks from predatory fish and killer whales induce massive predator-response patterns at the school level, including bend, vacuole, hourglass, pseudopodium, herd, split, and “tight-ball” formation within the shoal (Axelsen et al., 2001).

Many researchers reported social learning at a group level when, after observing predator responses of a neighbouring group, a school of fishes or a flock of birds react much more readily to the approach of a predator. For example, minnows showed a significant increase in the frequency of flight responses after observing the flight responses of minnows in a neighbouring tank that had been threatened by a predator (Magurran and Higham, 1988).

Cognitive aspects of social learning

Thorndike’s (1911) winged (but disputable) words “Apes badly ape” generate a series of questions such as “Do monkeys ape?” (Visalberghi and Fragaszy, 1990); “do rats ape?” (Byrne and Tomasello,1995); followed by Tomasello’s (1996) revision “Do apes ape?” to which I have add “Do ants ape?”. All these questions are derived from a discussion about which, if any, form of social learning is more intelligent. In particular,Whiten (2000) asks a question: Which is more intelligent? Imitation or emulation?

There is a growing body of evidence in literature that observational learning, irrespective of whether it includes imitation or "only" emulation or stimulus enhancement has cognitive implications. It is generally assumed that imitation is a more sophisticated cognitive process. It first of all concerns imitative translation process which includes cognitive implications of how organisms view the behaviour of others, relative to their own behaviour. It implies the ability to take the perspective of another. For this reason, researchers have tried to distinguish imitation from other kinds of social learning and influence. Recent reviews (e.g. Tomasello and Call, 1997) have concluded that only humans, or in some cases chimpanzees, can truly imitate. Emulation also demands feats of intelligence as it implies that the learner can select from the model's performance just the new information it needs, and then efficiently combine this information with its own practical knowledge to deal with the task in its own way.

There are several experimental paradigms for comparative studying cognitive aspects of social learning. A paradigm that is known as "do-as-I-do" test allows testing imitation as a process especially demanding variety of visual cross-modal performance (Heyes, 1993). Virginia and Keith Hayes (1952) gave intensive training to Viki, their young chimpanzee. They taught her by using an imitation set: whenever Vicki responded to the order "Do this, Vicki" by imitating the experimenter's actions, she was rewarded. Viki learned to respond correctly to the command "Do this!" over a broad class of behaviour. More recently, Custance, Whiten, and Bard (1995) replicated this result under more highly controlled conditions. The establishment of a "do as I do" concept not only verifies that chimpanzees can imitate, but it also demonstrates that they are capable of forming an imitation concept (Zentall, 2003).

An instrumental method that gives wider possibilities for comparative studies of social learning is known as the *two action method*, or *two-ways action/one outcome* as there are two possible actions which can be performed on one object. Imitation can therefore be tested by finding out whether subjects tend to perform whichever of the two actions they have seen. This can control for displays of other types of social learning such as stimulus enhancement and emulation. This method was first applied by Thorndike (1911) in his studies on chicks. Thorndike noted that those chicks which had a possibility to observe how their companions escape from a puzzle-box, coped with this task faster. He then divided demonstrating chicks into two groups, and trained each of two groups to escape by two different ways. Both ways were available for the observers. They, however, chose that way which they had seen from their demonstrator. This method has been developed in many studies. For example, Dawson and Foss (1965) trained budgerigars, *Melopsittacus undulatus*, to remove a lid from a cup using either their beak or their foot. When naive budgerigars were allowed to observe one of these techniques they showed a significant tendency to use the same method as their demonstrator.

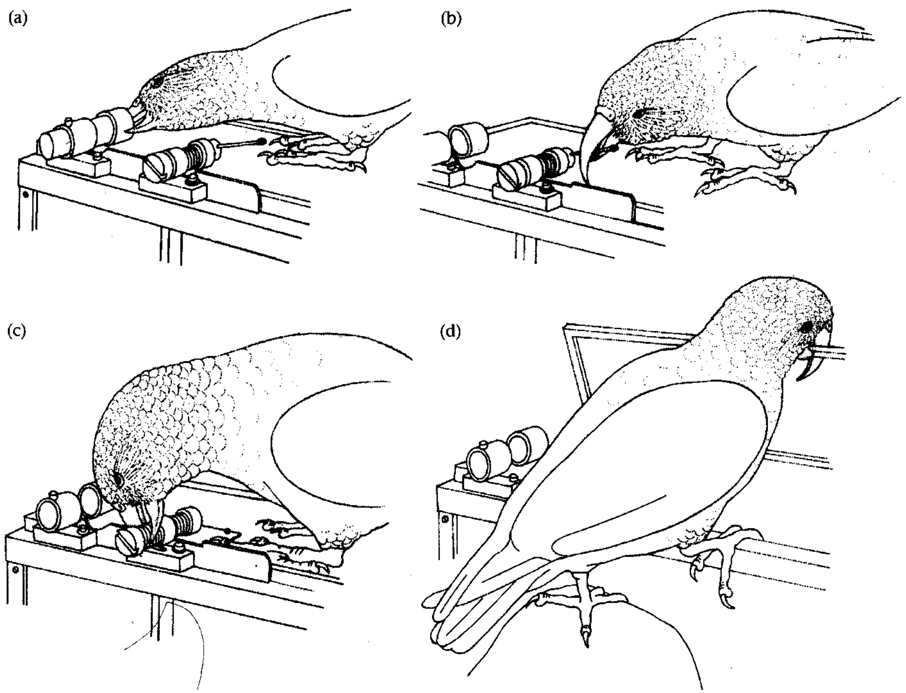
More recently, the two-ways action/one outcome paradigm was successfully used to show evidence of observational learning in many species, such as monkeys, rats, ravens and some others.

In order to examine cognitive aspects of more complex, sequence imitation, experimenters combine the two-ways action/one outcome paradigm with the use of *artificial fruit*, that is, a device that should be opened for food reward. To open the fruit, several defences have to be removed, as happens in many natural foods used by many species, especially, by primates and parrots. The artificial fruit may be of different levels of complexities, from a simple plastic container that can be easily opened, say, either by teeth or by extremities, to complex devices equipped with bolts, latches and so on. This combined method offers the possibility of a "gold standard" within comparative imitation research.

The use of the artificial fruit paradigm across different species led to the conclusion that some primates are more skilled imitators than others. In experiments of Whiten et al. (1996) chimpanzees and young children were presented with adult human models opening an artificial fruit in one of two alternative ways. In one experiments the defence consisted of a pair of bolts that had to be either poked out through the back, or pulled out at the front with a twisting motion to open the lid and to gain the edible treat inside. In another experiment a pin was spun round and removed using one of two different methods, after which a handle could be disabled by either pulling it out or turning it to one side, allowing the lid to be opened. Chimpanzees were found to copy the method they witnessed being used to remove the bolts, as did children. However, while the children also imitated the method of handle removal, the chimpanzees did not – all tended to use the same method of pulling out. Thus, in a situation when young children learned a technique with quite high fidelity, chimpanzees did not copy all they witnessed so faithfully. Further studies enabled researchers to suggest that, as it has been already noted before, the capacity for true imitation is restricted to humans and apes only, more precisely, to children and chimpanzees risen in a human environment.

It has been recently shown that autistic children display widely ranging imitation deficit whereas they do not differ from normal children in performance in emulation tests (Heyes, 2001). This enables to consider imitation a part of the normal development in our species which includes predisposition for copying actions of close company. It is interesting to note that cross fostering experiments revealed shifts to foster parents' behaviour just to that extend to what members of adopted species are predisposed for mimicking and imitation. This was clearly demonstrated on birds, and we can also recall an experiment in which a young fox performed species specific behaviour of his own species with only minor shifts to the behaviour of his foster mother, the dog (Mainardi, 1976). Similar results were obtained with ants raised by members of other species (Reznikova, 2001). As far as human infants are concerned, nobody could think about cross fostering experiments but there are some documentary evidences from abandoned children who grew up together with animals (in most cases, with dogs). These infants copied a number of behavioural acts from their companions: eating by licking, walking on four feet and using sounds similar to those of the dogs (Miklósi, 1999). Meltzoff (1988) argues that humans are genetically predisposed to imitate others, and this predisposition allows us to become an imitative generalists.

Huber and co-authors (2001) have investigated how social learning affects object exploration and manipulation in keas, *Nestor notabilis*. This New Zeland parrot, as the authors note, has been used as an example of curiosity in birds for a century, and its natural habitat is thought to have led to the evolution of extreme behavioural flexibility. Five young keas were allowed to observe a trained conspecific that iteratively demonstrated several techniques to open a large steel box. The lid of the box could be opened only after several locking devices had been dismantled: a bolt had to be pocked out, a split pin had to be pulled, and a screw had to be twisted out. The observers' initial manipulative actions were compared with those of five naive control birds (non-observers). Although the kea observers failed to open the box completely in their first attempts, they explored more, approached the locking device sooner and were more successful at opening them. These results provide evidence for effects of social facilitation and both generalised and local stimulus enhancement on object exploration in this species. The obtained data also suggest that the keas definitely learned something during observation. Although their initial attempts did not match the response topography or the sequence of model's actions, the birds' efficiency at unlocking the device seemed to reflect the acquisition of some functional understanding of the task through observation, that is, emulation learning.



PARROT

There was no evidence of true imitation in keas, and a salient explanation given by the authors is that the kea's propensity for exploration, object play and demolition runs counter to the exact reproduction of movements demonstrated by others. Keas are justly mentioned "chimpanzees among birds". Their dynamic and playful style of life does not coincide with close watching and imitating actions of others. Being attracted by a conspecific to explore a novel object does not necessarily lead to slavish copying but may lead to learning what parts of the object are worth exploring. Together with data on anthropoids, the cited results on parrots enable us to regard emulation learning as being cognitively quite demanding.

It is important for comparative imitation studies that many factors should be taken into account in order not to place a species into a list of "backwards". Among these factors, motivation is of great importance as well as ranking and "self-confidence" of individuals that play roles of demonstrators. For members of personalised animal societies it is important to copy actions of highly ranked individuals. It was taken into account in the Huber at al.'s work on keas cited above: highly ranked birds were appointed as demonstrators. Another example comes from Vanchatova's (1984) study in which imitation behaviour in capuchins *Cebus apella* was clearly demonstrated while in other studies this species were unable to learn to use efficiently a tool they had repeatedly observed being used by others. In Vanchatova's (1984) experiment the monkeys were highly motivated by a nature of a reward, that is, a little mouse to eat instead of items of vegetarian diet, and, what is not less important, it was the dominating individual who was used as a demonstrator.

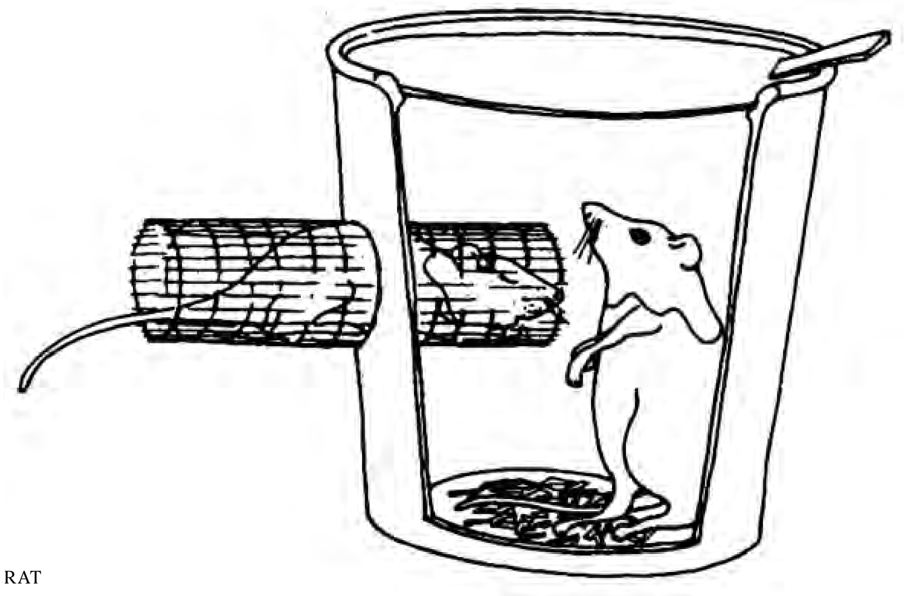
The Spread of Innovation within Populations

In laboratory studies experimenters create "innovators" by themselves. They choose active and exploratory animals that have high ranks in their groups, train them to solve a problem and after training let them to "inculcate" new knowledge among naïve members of social groups. This way of experimental investigation helps to enlighten a process of social learning and to estimate potentials of different species. However, such an approach does not give a possibility to learn how innovations spread within populations in the wild.

It is an intriguing question whether a single prodigy individual or may be several advanced individuals can propagate a new tradition in animal community. To catch sight of the transmission of novel behaviour in groups of animals, detailed observations in natural populations are needed, supplemented by experiments in captivity. Sometimes researchers are lucky to witness the gradual establishment of a new tradition. In the majority of cases described in literature new traditions concern vital situations such as feeding techniques or fear of predators. However, exquisite patterns of social behaviour such as specific modes of grooming or mating rituals can also serve as subjects for discussion.

The ways behavioural traditions spread. The phrase "population-specific behavioural traditions" is used to describe behaviours that have the following properties (Nagell, Olguin and Tomasello, 1993):

1. They are acquired through experience, rather than being innate.
2. They are found throughout a well-defined population.
3. They persist from one generation to the next.
4. They are absent in other populations of the same species.



RAT

The spread of novel feeding methods through a population, as a particular case of fixing population-specific behavioural traditions, has been documented for a number of terrestrial and avian species. Two of the most famous cases are milk-bottle top opening by birds in Britain (Fisher and Hinde 1949), and washing sweet potatoes (yams) by Japanese macaques (*Macaca fuscata*) (Kawai 1965). In both cases, the spread was initially thought to be due to imitation, but more recent work has cast doubt on this. Let us consider briefly these two examples together with some analogous studies which appreciate the role of simpler forms of learning than imitation.

Blue tits and great tits in Britain are notorious for their ability to break through the foil tops of milk bottles in order to drink the cream at the top. This skill is believed to have originated in a small group, and its spread to the rest of the population has been attributed to imitation. However, the results from a series of experiments by Sherry and Galef (1984) using black-capped chickadees, suggest that the spread of this habit was promoted by more simple than imitation means of social learning. If a bird should come across a bottle that has already been opened, it will drink the milk. Once it has drunk from the bottle, apparently the bird will be very much more likely to break through the foil tops in the future. Pavlovian conditioning provides one explanation for this outcome. Sherry and Galef (1990) report that their subjects were unlikely to open foil tops when they were tested in isolation. In an attempt to answer the question of how the birds came to open foil tops in the first place, experimenters examined the behaviour of a naive bird that had access to a foil covered container of cream when it could see another naive bird in an adjacent cage. The mere presence of this second bird was sufficient to encourage the first bird to peck at the foil cap and eventually open it. The experimenters consider social facilitation as the main mechanism responsible for the origins and perhaps spread of milk-bottle opening among certain birds. The reasons for social facilitation of pecking in this concrete situation are not fully understood, but the presence of the second bird may serve to reduce fear, or to encourage foraging responses, in the experimental subject.

An example of fixing of behavioural tradition in primates is provided by a group of Japanese macaque monkeys who wash sweet potato (yams) before eating them (Kawai 1965; Itani and Nishimura, 1973). In 1952, on the island of Koshima, scientists were providing a group of 22 Japanese macaques with sweet potatoes dropped in the sand. An 18-month-old female named Imo (note that in Japanese Imo means “potato”) found she could solve the problem by washing the potatoes in a nearby stream. Imo’s name has become legendary as one of the first personalized innovative animal described in scientific literature. The researchers also scattered grains along the beach. The monkeys had to pick the grains from the sand, one grain at a time. Then Imo threw a handful of sandy grain in the water. The sand sank and the grain floated, making it easy to scoop up. Again, other members of Imo’s troop eventually learned how to throw their grain in the water. By 1962, almost all the monkeys in the Koshima troop were observed to be washing their sweet potatoes.

Nagell et al. (1993) have suggested that the spread of this habit is due in part to stimulus enhancement. The attention of a naive monkey can be drowning to a potato when it sees another monkey to pick one up. The naive monkey may then pick up its own potato and for social reasons follow the experienced monkey into the river. At this point, the naive monkey may learn by accident the benefits that accrue from placing the potato in the water.

Indeed, stable embedding of new feeding technique in wild populations does not necessarily mean that there is imitation underlying cultural transmission. Behavioural habits can be based on mechanisms of social learning which

CROW

are simpler than imitation. For instance, stimulus enhancement explains the acquisition of pine-cone stripping behaviour of black rats. Terkel (1996) found that although naive rats never learned to strip cones unaided, the animals were capable of learning the trick if partially striped cones were provided, and especially so if they were exposed to cones with progressively fewer rows of scales removed. Young rats pay close attention to whatever their mother is eating, and often manage to steal partially-eaten cones from her.

Combination of social facilitation, stimulus enhancement and individual learning are likely to underlie forming of "subcultures", or behaviourally specialised "cultural clans" in animals. There are many examples in literature. For instance, populations of crows in Kamchatka specialise in different techniques of getting food from humans. Some flocks regularly steal alms at cemeteries whereas others track skiers in winter and gatherers of mushrooms in summer stealing food from them when they make stops. Dolphins in Shark Bay show a similar specific foraging specialisation – feeding by humans at Monkey Mia beach – in which not all of the population takes part. This variation appears to be maintained by vertical cultural transmission, since most of the dolphins taking advantage of the feeding are offspring of females which were themselves fed (Smolker et al. 1997); hence the specialisation is likely learned while swimming with the mother. Clans of Norway rats specialise on catching fishes or frogs, stealing fishes from fishing nets, harvesting molluscs, and stealing eggs and chicks from birds' nests. Clans dwelling on different sides of a lake display different techniques of catching frogs. Galef (1985) conducted laboratory experiments simulating his own observation in nature on how Norway rats dive for molluscs. It turned out that young pups are able to adopt this technique from their mothers.

Being lucky to catch first manifestations of novel behaviour within a wild population and then monitoring it during long periods, several researchers have reported on very interesting cases of inculcation of new habits, mainly, feeding technique. For instance, the regular cracking of palm tree nuts with the aid of two stones ("hammer" and "anvil") by Japanese macaques was fixed from the very first case and then monitored for 20 years. During this time, about 80% of population had adopted this method (Huffman and Nishie, 2001). Spread of a novel feeding technique was described in humpback whales (Rendell and Whitehead, 2001). In the southern Gulf of Maine, a novel complex feeding technique, "lobtail feeding", was first observed in 1981, and by 1989 had been adopted by nearly 50% of the population. Not only new feeding techniques can

be transmitted socially. Social transmission can also apply to group-specific vocalizations, courtship displays, and grooming postures and so on (McGrew and Tutin, 1978; McGrew, 2004). How it is to be an innovator. As we have already seen from the analysis of examples of innovative behaviour, the main body of data concerns the use of new food or application of new feeding techniques. Some authors consider the frequency of innovative behaviours, for a given taxonomic group, a useful indicator of its behavioural plasticity and its tendency to use novel means to solve environmental problems.

Lefebvre et al. (1997) collected 322 foraging innovations in avian species from nine British and North American ornithological journals and analysed them in connection with measures of relative forebrain size. Innovations were documented from field studies and included such examples as, for Herring gull, catching small rabbits and killing them by dropping on rocks or, for House sparrow, systematic searching of car radiator grills for insects. The authors found that relative forebrain size in different species was related to innovation frequency in the two zones, the British Isles and North America. It seems that at a taxonomic level of innovative behaviour demands at least relevant brains.

What about characteristic features of innovators at the individual level? What individual dispositions required for becoming innovative? Only little is yet known yet about the starting conditions of innovations. For example, in a study with guppies, *Poecilia reticulata*, in which fishes had to quickly make a choice between holes in a partition of an aquarium, Laland and Reader (1999) found that females were more likely to innovate than males, smaller fish more likely than larger fish and food-deprived fish more likely than non-deprived.

The expression of individual behavioural and physiological phenotypes or *coping styles* is defined as the way to cope behaviourally and physiologically with environmental and social challenges. The existence of different coping styles could be shown for various animal species including humans (Broom, 2003). In mice and rats, for example, aggressive individuals ("proactive copers") entrained more rigid routines, spent less time exploring novel environments and were less alert to changing stimuli in known environments than less aggressive individuals ("reactive copers"). Similar patterns were found in many species such as great tits, domestic pigs, cichlid fish, and others (see Broom, 2001, for a review). In ants scouting individuals that can first solve complex searching problems and usually attract foragers to novel objects, have smaller size, more diverse behavioural repertoire, and they are much more agile than other members of their colony (Reznikova, 1982; Reznikova and Ryabko, 1994).

Experimenters at Konrad-Lorenz Research Station in Grunau had investigated the spread of the ability to trigger a food dispenser in a free-living, semi-tame flock of greylag geese, *Anser anser*, for several years (Fritz et al., 2000; Pfeffer et al., 2002). The researchers investigated hormonal and behavioural correlates with the individual's ability to perform operant tasks in hand-raised greylag goslings. Results suggest that becoming an innovator may be contingent upon individual coping styles. A tendency was revealed that males are more successful in coping with new tasks whereas females are biased toward learning by means of stimulus enhancement. Individuals that displayed elements of innovative behaviour possess higher level of corticosterone than conservative geese.

These, yet limited, data enable us to suggest that predisposition to innovative behaviour is based on some definite genetic features. In changeable environment wide spectrum of adaptations is tested for defects and this includes behavioural adaptations. As McGrew (1992) noted, in many situations when researchers fixed innovations within populations, they could be predicted basing on essential change in environment such as shortage in food, forced migrations and so on. Under such circumstances new customs "invented" by few innovators can be more useful and adequate than species specific stereotypes that had been valid before. However, this does not mean that members of community will readily copy the novel life style. Usually animals observe odd behaviour of their conspecific curiously but keep aloof. Do innovators try to spread new behavioural pattern, in other words, can animal teach each others?

Can animals teach? Active tutoring ("teaching") can be considered the most complex form of sharing knowledge in animal communities. A working definition of teaching widely accepted among students of social learning was suggested by Caro and Hauser (1994): "An individual actor (A) can be said to teach if it modifies its behaviour only in the presence of a naive observer, B, at some cost, or at least without obtaining an immediate benefit for itself. A's behaviour thereby encourages or punishes B's behaviour, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all".

There are two main processes of transferring information within populations in which tutoring can be involved: (1) polishing of species-specific behavioural patterns and (2) spreading of innovations. Both processes are parts of social learning. Back-fitting of species-specific behaviour by efforts of tutoring parents is quite usual in animals, first of all, in vertebrate predators. In many species polishing of searching and hunting behaviour makes up an integral part of their ontogenetic development.

However, tutoring as an instrument for spreading innovations is a rare phenomenon in wild life. One can say that this concerns a level of complexity which is over and above the "general plan" of species-specific behaviour. The fact is that innovations can spread within populations by means that are simpler than tutoring. We have already seen this from previous sections and will consider in the last section of this chapter. Although the real role of tutoring is not great, the analysis of teaching in animals is very important for estimation of limits of their cognitive abilities. Even isolated observations on instances of teaching in the wild are valuable.

There is a large body of data about how predators teach their offspring to kill victims. This concerns predators of different sizes and styles of hunting, from giant whales to little jerboas. At the same time, it is known that members of many species grow up as self-made hunters. For instance, polecats (*Putorius putorius*) learn very quickly how a mouse must be grasped by the neck so that it cannot bite back. During normal ontogenesis complex hunting behaviour can mature with the assistance of individual experience. It can be considered a complex process because innate releasing mechanisms mature as well and they become increasingly more selective through individual learning. This scenario is widely distributed in animal species which can be illustrated by Eible-Eibesfeldt's (1970) examples of the prey catching behaviour of toads, frogs and others. Even in such advanced hunters as Mustellidae parents' instructions have little part. If so, is that necessary for predators to teach the young? Is it possible that parents' instruction run idle in animals? Special investigation is needed in each case if we want to know whether parents take part in shaping of a character of a wild hunter. Let us consider several examples.

It has been known for a long time that in felids and other carnivores' mothers modify their predatory behaviour in a series of stages. It was described by Leyhausen (1979) in domestic cats *Felis catus*. Adult females pursue, capture, kill and eat prey in a smooth sequence with little hesitation between acts. However, when cats become mothers and their kittens start walking out of the nest, mothers alter their behaviour and carry prey to their kittens to eat it in front of them. Next, they carry live prey directly to their offspring and allow them to play with it but recapture it if it escapes. Finally females take little part in prey catching at all, merely moving toward prey initially while kittens chase, capture and dispatch it efficiently. Mothers give characteristic mewing calls to their kittens in all of these situations.

The sequence of mothers' acts is so logical from a human point of view that it undoubtedly looks like successive shaping of the youngs' hunting behaviour. Under controlled laboratory conditions Caro (1981) tested the alternative hypothesis about the role of mother's teaching in shaping hunting behaviour in kittens. In Caro's study kittens between the ages of 4 and 12 weeks were exposed to domestic mice as a live prey. In one series of trials mother cats were present, while in other trials the mothers were absent. Control kittens received identical exposures but without their mothers being present. Behaviour of mothers was also recorded. The obtained results suggest that maternal behaviour reduces the age at which kittens acquire predatory skills. For instance, when six month–old kittens were tested on their predatory abilities, experimental subjects delivered significantly more bites to the nape but not to other regions of the mouse's body than did control kittens, that is, they more easily applied the method by which adult cats dispatch rodent prey. However, Caro (1981) found it hard to say whether maternal behaviour is sensitive to developmental changes in kitten behaviour. These two processes seem to go in two parallel courses. Indeed, the timing of each step in the mothers' predatory sequence might not be contingent upon improvement in their cubs' predatory skills, but rather change according to their individual time course. Certain mothers started to leave prey with their kittens at very early stages when the young were not able to react to it. Many aspects of mother's predatory behaviour were significantly negatively correlated with increasing skills of their offspring. Caro (1987, 1994) then has continued with studying of interactions between mothers, cubs and prey on wild cheetah in the Serengeti National Park, Tanzania. The researcher found a very slow progress in young cheetah's education seemingly as a graduate result of maternal great efforts. It turned out that cub's hunting skills remain poor up to and beyond independence from their mother, showing surprisingly little improvement in the ten months after first being introduced to prey. In sum, Caro's data enable us to be careful with the conclusion that this is just maternal tutoring which make cats skilled hunters.

A good example that illustrates how difficult it is to judge about the roles of maturation and investments of parents in shaping of hunting behaviour, is the behaviour of ospreys *Pandion haliactus*. Meinertzhagen (1954) provided rich description of adult ospreys encouraging their fledglings to catch fishes. At first, the adult perched away from the nest with fish in their talons but would not feed the young, despite their screaming for food, repeatedly flying away with an apparent attempt to encourage the young to follow. On the first day the fledglings did not leave the nest, but on the next two days when the young flew off the nest to a rock, they were fed. On the following day, the young followed the parents to hunt over a lake. Each fledgling caught a fish, carried it toward the young and then dropped it, but caught it again and secured it before it hit the water. After having repeated this many times, one of the young finally caught the fish in a stoop and carried it to the rock to eat it. The less successful sibling now flew to the rock to share the catch, but the parent arrived and literally pushed this offspring off the rock forcing it to take wing again. The process of dropping a fish was repeated until the second fledging finally caught it and went back to the rock to eat. On the fifth day the same procedure was observed with each fledging following a parent around and unsuccessfully attempting to catch fish that were dropped for it in midair. When the fish reached the surface, the parents would retrieve it until eventually youngsters descended to the water and picked up the fish. On the seventh day, the adults drove the offspring away from the lake and they were not seen again. So, the period of education took six days.

Seemingly, this study provides a strong evidence of a definite role of parental teaching in the building of the hunting behaviour in osprey. Nevertheless, observations of hand-raised young ospreys showed that they successfully caught fishes within three days to three weeks of being released into the wild, in the absence of parental instruction (Schaadt and Rymon, 1982).

These data enables us to suggest that parental "instructions" run in parallel with maturation of hunting behaviour of young, and that at least one aspect of the use of parental teaching in animals is to awake dormant behavioural patterns; repetition of instructions in mammals and numbers of encounters with successful hunters in ants possibly have a cumulative effect. This does not mean that teaching should be excluded from consideration of ontogenesis of hunting behaviour.

Transmission of innovations by teaching. Active teaching as a mean for sharing new experience would seem to be very rare in animal kingdom, even in apes. The great role of imitation in social life of anthropoids does not necessarily means that they can teach each others. Young chimps learn how to break twigs from trees, strip away the leaves, and insert them into termite holes by observing adults. The steps required to extract termites in this manner are lengthy and complex. Without the demonstrations of adults, many chimps would probably never become very successful termite fishers. However, part of the acquisition of this tool use appears to relate to innate characteristics of chimpanzee behaviour. All young chimpanzees amuse themselves by playing with sticks and poking them into holes. It seems as though the chimps are able to observe the more skilled adults and translate their juveniles play into a successful means for securing food. But this does not mean that young chimpanzees follow instructions of adults (Goodall, 1986).

During ten years of investigations Boesch (1991) observed interactions between mothers and their young among Tai chimpanzees in the context of nut cracking. He divided his observations of mother-offspring inter-relations into "stimulation", "facilitation" and "active teaching". Observations of stimulations and facilitation included such things as mothers' leaving intact nuts for their infants to crack (which they never did for other individuals) or placing hammers and nuts in the right position near the anvil for their infants to use. Stimulations were observed on 387 occasions of interactions between mothers and their children. Stimulation differs from the common behavioural pattern for adult chimpanzees, when they carry their hummers during nut collection and consume the nuts that they have placed on an anvil. Mothers incurred a foraging cost by having to find more nuts and another tool for opening them.

Active teaching was observed only twice and involved direct intervention on the part of the mother in her offspring's attempt to crack open a nut. In one example, a six-year-old male had taken a majority of his mother's nuts, as well as her stone-hummer. After the young male placed a nut on the anvil, but prior to opening it, his mother approached, picked up the nut, cleaned the anvil, and put the nut back in a different position, more suitable for opening. The young male cracked the nut and ate the kernel. In the second example, another mother reoriented the hummer for her five-year-old daughter who then succeeds in opening several nuts by maintaining the same grip on the hummer that her mother had used.

One more example of isolated cases of teaching in animals came from the experimental investigations on free-living scrub jays, *Aphelocoma coerulescens*, by Midford et al. (2000). Experimenters trained models (demonstrators) and then followed them as they modelled the task in the presence of naïve (observer) animals. Jays had to learn that a class of objects (bright plastic rings) indicated the presence of buried food (peanut peaces) in a specific location, the centre of the ring. Birds were trained in their family groups to perform the task during summer season, and were allowed to perform the task in the presence of juveniles in later years. Jays living in 18 control families received partial exposure to the training situation, but received no exposure to the ring before being presented with the task in the presence of their young. Juveniles in 16 families with trained jays were able to witness demonstrations and to scrounge peanut peaces from the models as they completed the task. These 41 juveniles learned much more of the task than the 33 juveniles in control families. What is important for our narrative is that the authors observed three cases of active teaching in two separate families. In each case, the highly ranked bird (the breeder of the family) dug in a centre of a ring until it uncovered the food. Then, rather than taking the pieces of nuts, the adult either departed or stood over the depression it dug, pointed its bill downwards, towards the pieces, until the juvenile took them. This differs markedly from the usual behaviour of jays after finding bits and, as the authors give this, fall within the definition of teaching.

Culture in Animal Societies

In this paragraph we will briefly analyse a complex and fascinating problem of what is culture in animals. The relationship between cultural and genetic evolution was identified by Wilson (1975, 1998) as one of the "great remaining problems of the natural sciences". Several studies, adopting Dawkins' (1976) concept of the "meme" as the unit of cultural evolution, have examined factors influencing the transmission and success of memes in animal cultures. The presence of cultural processes within animal societies is an area of some controversy. How to treat cultural behaviour in animals much depends on its definition. Many definitions in literature attribute cultural traits only to humans. At the other end of the scale is considering culture as a "meme pool" in populations which can include all cases of the regular use of public information in populations basing on very simple forms of social learning.

Many cognitive ethologists agree now that human beings are biologically adapted for culture in ways that other primates are not, as evidenced most clearly by the fact that human cultural traditions accumulate modifications over historical time. Our species is likely to possess some uniquely powerful forms of cultural learning, enabling the acquisition of language, discourse skills, tool-use practices, and other conventional activities.

Not arguing about restricted notions of "culture" in animals, I would rather adhere to broad definitions basing on social learning as the main mechanism of "cultural transmission" of behavioural patterns in animal societies. I see here a fascinating perspective of estimating limits of power of social learning in non humans that allow some species to improve adaptiveness of behaviour by non genetic means. In this context, I consider the broad definitions as acceptable such as "culture is information or behaviour acquired from conspecifics through some form of social learning" (Boyd and Richerson 1996), and "animal tradition that rests either on tuition of one animal by another or on imitation by one animal of acts performed by another" (Galef, 1992). Defining culture as a package of behaviours, the working description given by Nishida (1987) is useful: "Cultural behaviour is defined as behaviour that is (a) transmitted socially rather than genetically, (b) shared by many members within a group, (c) persistent over generations and (d) not simply the result of adaptation to different local conditions".

Empirical approaches for studying animal culture. The empirical study of cultural processes in animals is generally approached in two major ways: controlled laboratory experiments on mechanisms of social learning and field descriptions of behavioural variation (Lefebvre and Palameta, 1988). Both make important contributions to our understanding of culture.

The first approach focuses on experimental study of the cognitive processes underlying cultural transmission. In general, controlled laboratory experimentation is a preferred methodological tool; this gives the approach the advantage of controlled conditions and hence less chance of ambiguity in the interpretation of data. However, the studies do not necessarily relate to what occurs in the wild.

The second approach is field-based; here culture is deduced from patterns of behavioural variation in time and space, which cannot be explained by environmental or genetic factors (Whiten et al. 1999). This approach has been likened to ethnography in the social sciences, and thus is called "ethnographic approach" in recent ethological literature. Practically, students of chimpanzees, the most "cultural" after our species, have elaborated the following steps to identify cultural variations: 1) to show that behavioural differences between chimpanzee populations are not consistent with a genetic explanation – for example, where a boundary between different methods of tool use occurs within the range of a sub-species (e.g. at a large river), rather than between sub-species; 2) to check that the behavioural differences cannot be explained by ecological factors such as availability of suitable raw materials for making tools; 3) to study the transmission processes used by animals in controlled experiments: can they learn by watching others? If so, what kind of things do they learn? Well designed experiments of this kind can guide researchers to the most likely learning mechanisms at work in the wild.

"Hearths of culture" in animal societies. We argue about cultural changes in animal societies in those cases when animals learn new living habits and pass them along to the next generation. In such a situation spread of a certain innovation results in stable conservation of a new custom that is further maintained and transmitted in a train of generations through social learning. Culture thus is displayed as the presence of geographically distinct variants of habits. Even in this limited sense, culture was long considered to be a uniquely human trait. Ethologists have investigated the problem of animal culture for decades but only in the last few years a clear picture of cultural diversity in several "elite" species begun to emerge. Insight into cultural evolution came from comparative geographic approach when researchers have thoroughly studied behavioural customs in different populations and thus revealed "hearths of culture" in animal societies.

The main methodological difficulty on the way of studying animal culture is to recognize innovations in the field. Even when the origin of a certain innovation had been observed, it is difficult to predict a living trajectory of this innovation. As it has been noted earlier in this chapter, innovations can be spread by means of relatively simple forms of social learning and even low-end innovations can lead to extensive cultural change. Remember Japanese macaque potato washing. By using the water in connection with their food, the Koshima monkeys began to exploit the sea as a resource in their environment. Sweet potato washing led to wheat washing, and then to bathing behaviour and swimming, and the utilization of sea plants and animals for food (Kawai, 1965).

At the same time, there are reasons to believe that new skills do not spread easily in animal populations. As Kummer and Goodall (1985) note, of many innovative behaviours observed, only a few will be passed on to other individuals, and seldom will they spread through the whole troop. For example, Goodall (1986) observed two instances of using stones by adolescent chimpanzees to kill dangerous insects. She supposed that usage of stones should become customary in that reference group. But this had not happen in the following thirty years, the innovation faded away.

The chimpanzee is clearly the most interesting animals from a cultural point of view. Different populations of chimpanzees seem to have their own unique behavioural repertoires, including such things as food preferences, tool use, gesture signals, and other behaviours, and these group differences often persist across generations. After collecting a great body of data in the wild, the first intimation that chimpanzee possess "material culture" came with McGrew's (1992) book about chimpanzee's tool use. Since then, new observations have appeared and some researchers have argued that individual communities of chimpanzees have their own local traditions. The grand synthesis was done by a collective of primatologists published in Nature (Whiten at al,, 1999; see also a review by de Waal, 1999).

The researchers discovered the various habits of chimpanzees at seven field sites and clearly distinguished 39 culturally transmitted behavioural patterns. Some of them concern tool use, such as ant dipping, termite fishing, nut cracking, honey dipping, drinking water with leaves, and so on. Others concern characteristic behavioural habits such as rain-dances, hand-clasp grooming, details of courtship rituals, and so on. For example, some populations fish for ants with short sticks, eating insects from the stick one by one. Only in one population apes developed the more efficient technique of accumulating many ants on a long rod, after which all insects are swept into the mouth with a single hand motion. Another impressive difference concerns leaf-using for drinking water. In different communities chimpanzees use "leaf sponge" crumbling leaves in their mouth, soaking them in tree hollows with their hands, and sucking the water from them. The other type is "leaf spoon" where apes use leaves like a spoon, without crumbling them up, to scoop out the water.

Until recently chimpanzees were considered the only species among great apes that possess elements of "material culture". Nowadays researchers consider chimpanzees displaying the highest level of manufacturability but not a single species sharing with human the membership in the club of animals with culture. Besides Africa's gorillas and chimpanzees great apes include orangutans, the fabled red apes of the forests of Indonesia. Orangutans *Pongo pygmaeus* are less social than other primates, living a rather solitary life in the wild. They are slow in movement, not leaping vigorously from limb to limb like chimps or crashing through underbrush like the gorilla. Thirty years of field observations of the shy Southeast Asian orangutan allow the international group of researchers to conclude that these apes definitely have the ability to adopt and pass along learned behaviours (van Schaik et al., 2003).

Studying six populations of orangutans in Borneo and Sumatra, Indonesia, researchers identified 24 examples of behaviours that have been defined as cultural variants. Many of the culturally transmitted behaviours involve tool use such as using sticks to dig seeds out of fruit, to poke into tree holes to obtain insects, or to scratch; using leaves as napkins or as gloves to protect against spiny fruit. Twelve other behaviours, such as making a pillow with twigs, were seen only rarely or were practiced by only a single individual. The practices common in one group and absent in another are of great interest to researchers because variations on these behaviours found among the different populations seem to be cultural. For example, in a Sumatran swamp, one particular group of orangutans like a fruit that was protected by needle-like spines, and to get to the edible seeds inside, the apes used a tool. With a sharp stick, they pried open the fruit to extract the seeds. Only a single group of the six observed has discovered how to use sticks to extract insects from tree holes or to wedge out seeds from fruits. Such tool use is common among chimpanzees, but the Sumatran orangutan band puts a unique twist to the practice – they grip the stick with their teeth instead of their hands. On the far side of the river another group of orangutans have plenty of sticks available, but they do not use them on fruit; most ignore the fruit, others smash it to get the seeds. The stick trick seemed to be an invention created by one group that was passed along. This is what researchers call "a cultural boundary".

Recent data obtained by Krützen et al. (2005) allow adding marine mammals to the catalog of culturally transmitted forms of tool use in nonhuman populations. In Shark Bay, Western Australia, wild bottlenose dolphins (*Tursiops* sp.) apparently use marine sponges as foraging tools. Sponge carrying came to the attention of scientists 20 years ago when a boater reported seeing a dolphin in Shark Bay with a "tumor" on its beak. The tumor turned out to be a sponge, and in 1997 researchers proposed sponge carrying as the first known example of tool use in dolphins (Smolker et al., 1997). Dolphins have devised a way to break marine sponges off the seafloor and wear them over their snouts when foraging. Researchers believe that dolphins use sponges as a kind of glove to protect their sensitive rostrums when they probe for prey in the substrate. Unlike in apes, tool use in this population is almost exclusively limited to a single matriline that is part of a large albeit open social network of frequently interacting individuals. The researchers conclude that the behaviour is culturally transmitted, presumably by mothers teaching the skills to their sons and daughters, although they have not actually observed this feat in action.

Tool-use is the most amazing but not a single population-specific behavioural trait enabling cetacean biologists to claim that marine mammals possess culture (Whitehead, 1998; Decke et al., 2000) or at least traditions. Field researchers listed many population-specific patterns concerning foraging strategies, styles of diving and other behavioural traits many of them have been clearly demonstrated as transmitted by means of social learning (for a review see Mann et al., eds., 2000).

Conclusion

Social learning plays an important role in the processes of “tuning” behaviour in group living species and in those which live solitary but at least have contacts with relatives at early stages of ontogenesis. Readiness to gain information from conspecifics reflects both the conformity prevailing in animals’ society and the flexibility that enables animals to improve their individual behaviour in changeable environment.

Capabilities of learning from others and about others allow members of species to decrease the cost of being equipped by inherited suite of a great number of behavioural characteristics. Being extra guided by means of social learning, animals can increase their fitness and make relationships with their environment more flexible and thus more adequate. It is possible that social learning has more fundamental importance as a part of evolutionary strategies of many species than we thought before.

Animals’ ability to develop completely new behaviour by observing innovations invented by a single or a few advanced individuals should be based on intelligence rather than automatic population processes. Effectiveness of new behaviours performed by “wild prodigies” may be evident for conspecifics but this does not mean that many imitators will subscribe to the same activity. Usually animals observe innovators and try to stand aside. Innovations are most often extinguished within a viscous environment of wild minds. One can say that non-humans badly teach and poorly learn, and that preparedness is the best teacher for animals.

It is very likely that, as Premack and Premack (1996) give this, humans possess unique “pedagogic disposition” to exploit the learners’ “predisposition to culture”, for teachers to demonstrate correct performance for the benefit of the learner.

In general, social learning is based on difference between members of animal communities, that is, on behavioural specialisation in populations, and in some situations, on cognitive specialisation of individuals.

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